FINAL REPORT

Linking Conservation Actions with Population Viability Models: Reducing Uncertainty to Better Predict Management Effects on Viability

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The overall objective of this program was to develop a set of models and methods for prioritizing management of threatened, endangered, and at-risk species. Specifically, we sought to develop tools for evaluating effects of management on population viability using varying levels of data: 1) life history data when little is known about a species, 2) count data when only estimates of abundance through time are available, and 3) metapopulation models when we have a lot of demographic data about multiple populations.

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LIST OF ACRONYMS

AIC   Akaike's Information Criterion
ASY   After Second Year
BMGR   Barry M. Goldwater Range
CCBT   Chorro Creek bog thistle
CPNWR   Cabeza Prieta National Wildlife Refuge
DoD   Department of Defense
DPNP   Departure from normal monthly precipitation (mm)
DPTP   Departure from normal monthly temperature (^{o}C)
DSP   Deterministic Single Population
EGOE   Exponential Growth with Observation Error
EGPN   Exponential Growth with Process Noise
EGSS   Exponential Growth State-Space
FAST   Fourier Amplitude Sensitivity Test
GCWA   Golden-Cheeked Warbler
GSS   Gompertz State Space
HY   Hatch Year
IUCN   International Union for the Conservation of Nature
LHT   Life History Typology
MFA   Mean Final Abundance
NMFWA   National Military Fish and Wildlife Association
OAT   One at a Time
PIM   Parameter Index Matrix
PVA   Population Viability Analysis
RCS   Recovery Credit System
SMP   Stochastic Metapopulation
SSP   Stochastic Single Population
SY   Second Year
T&E   Threatened and Endangered
USFWS   U.S. Fish and Wildlife Service
VPM   Viable Population Monitoring
YTC   Yakima Training Center

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ABSTRACT

Objectives: The overall objective of this program was to develop a set of models and methods for prioritizing management of threatened, endangered, and at-risk species. Specifically, we sought to develop tools for evaluating effects of management on population viability using varying levels of data: 1) life history data when little is known about a species, 2) count data when only estimates of abundance through time are available, and 3) metapopulation models when we have a lot of demographic data about multiple populations.

Technical Approach: We first constructed a framework based on structured population models that can be used to evaluate possible effects of management actions on population growth rates for data-poor species. We demonstrated this approach with the arroyo toad. We then used time series of count data to fit stochastic models of population growth and assess population trend or viability, and applied the approach to evaluate extinction risk for greater sage-grouse at Yakima Training Center. For species with detailed information about vital rates, spatial structure, and metapopulation characteristics, we developed methods for conducting global sensitivity analyses of viability models for multiple populations. We demonstrated these methods using a pilot conservation incentive program for golden-cheeked warblers at Fort Hood. Finally, we combined time-series abundance estimates for multiple populations to evaluate probability of persistence for Sonoran pronghorn at Barry M. Goldwater Range.

Results: We demonstrated that arroyo toad population growth rates are highly dependent on survival of toads during their terrestrial life stages. We also illustrated the strong effect of parameter uncertainty on population persistence estimates. We next applied a set of population growth models to the greater sage-grouse population at Yakima Training Center and showed that the population growth rate is negatively influenced by drought and increasing area of grassland habitat. Overall, the probability of this population dropping below an extinction threshold of 50 lekking males was high under the best growth models. In demonstrating our approach for applying sensitivity analyses to metapopulation models for golden-cheeked warblers, we found that uncertainty in model structure and parameter estimates made it impossible to develop general guidelines for valuing habitat patches, but we identified parameters that need to be targeted in future research. Using time-series estimates of abundance for multiple populations, we estimated the probability of persistence for Sonoran pronghorn under three management scenarios and showed a clear and substantial benefit to supplementing the wild population with individuals from the captive population at Cabeza Prieta National Wildlife Refuge.

Benefits: The demonstrations of our approaches were designed to address real management issues and have clear and immediate use to the managers of focal installations. The general tools we've developed can be used to address management questions for many species of DoD concern and can be used to improve biological assessments, NEPA analyses, recovery planning, and endangered species management plans. Moreover, these tools can be used to provide direction as to how future research should proceed to focus on the factors that are most important to population viability.

INTRODUCTION

The primary mission of most federal agencies does not include protection of imperiled species. The mission of the Department of Defense (DoD), for example, is to provide military forces necessary to protect the security of the United States. Yet a variety of laws and regulations demand that planning and implementation of actions to support military readiness take into consideration their effects on species and habitats of concern. Natural resource managers are thus continually challenged to evaluate the effects of a wide range of activities on species of concern in a world of limited time and financial resources. Compounding the challenge are the frequent shortages of data needed and the complexity of most quantitative approaches for in-depth effects analyses. Of necessity, then, these evaluations are typically qualitative and based largely on expert opinion. The manager's job would be greatly facilitated by easy to use, scientifically-based tools to assess effects of training and conservation programs on the viability of imperiled species.

In this report, we describe an approach that links quantitative population ecology with biological data and management alternatives. A key element of our approach is a set of tools for assessing effects of training and conservation that, for a given species, are appropriate to the amount of biological data available. Each tool is based in population modeling and provides a quantitative platform for evaluating population viability under different management scenarios. As the level of available data for a species increases, more complex and powerful analyses are possible. However, each tool is designed to be used by biologists without extensive training in quantitative ecology or modeling.

A useful approach to determine how management actions will influence the viability of a species is to model population dynamics and quantify the effects that various actions have on extinction risk. Collectively, these quantitative approaches for evaluating extinction risk are captured in the set of population viability analysis (PVA) methods. PVA can be defined as the application of data and models to predict a series of likelihoods that a population will persist for specified times into the future and includes three inter-related components: persistence (extinction or quasi-extinction), persistence time, and likelihood of persistence (Mills et al. 2005). Considering these components, PVA must be conducted as an examination of alternatives (i.e., management actions), with a range of data and products, instead of performing a single PVA for a species with "X" data for "Y" probability of persistence over "Z" years. For listed species, PVA can be used to compare probabilities of persistence across a range of management alternatives and metapopulation configurations (e.g., number and sizes of populations), leading to practical, effective management programs to support recovery (Possingham et al. 2002).

Many key aspects of PVA have a strong biological basis, but the selection of goals requires the addition of a social component. Issues such as "For how long do we want to

evaluate persistence?" and "How secure should persistence be?" require social, cultural, economic, and political considerations (Scott et al. 1995, Shaffer 1987, Ludwig and Walters 2002) and would benefit from incorporating a mechanism for acquiring information from a large array of sources. Scott et al. (1995) proposed that when PVA is used in endangered species recovery planning it should incorporate short-term projections that are evaluated over time against a long-term goal (see also Goodman 2002, Reed et al. 2006). The long-term viability assessment should include goals that are biologically based. The short-term projections should explicitly incorporate political/legal/social constraints; monitoring and the iterative application of short-term PVAs can be used to evaluate how well long-term goals are being achieved. Thus, public review (and political tradeoffs) can be incorporated in choosing short-term management strategies, but ultimate success is judged against the yardstick of the long-term, biologically based goal and legally defensible recovery objectives.

One of the most powerful approaches to PVA is the construction of demographically explicit models of population growth. This class of PVA models uses estimates of vital rates (i.e., age-specific survival and fecundity) and allows for consideration of environmental and demographic stochasticity, density dependence, and can be expanded to incorporate metapopulation dynamics. Although these models require difficult-to-obtain information, they have the advantage of assembling biological information in a way that suggests specific actions that might reduce the chance of extinction (Beissinger and Westphal 1998). There are a variety of different model structures for conducting a demographically-based PVA with each carrying its own set of assumptions and data requirements (Beissinger and Westphal 1998). At one end of the spectrum are simple deterministic matrix models applied to a single population (DSP). These models require the least amount of empirical data for specifying model parameters and although they are not technically a "PVA" model since no extinction risk is calculated, they are often used to inform conservation decisions of imperiled species. A key simplifying assumption of DSP models is that demographic rates remain constant or nearly so through time. When there is significant temporal variation in these rates, population viability can be greatly affected by not only mean demographic rates but also their variability. To deal with these effects, stochastic models are often used. Stochastic single-population models (SSP) allow matrix parameters to vary as a result of environmental and demographic stochasticity. Both DSP and SSP models treat all individuals as belonging to the same population with equal demographic rates for DSP models or equal distributions of demographic rates for SSP models. However, in many situations it is more realistic to assign individuals to subpopulations that are distributed across the landscape and are connected by dispersal or correlated demographics. Each subpopulation is allowed to have independent, within the correlation structure, demographics as well as rates of immigration/emigration. To model these situations, stochastic models that incorporate relationships among multiple, spatially segregated sub-populations have been developed (stochastic metapopulation models; SMP).

In an ideal world, data would be easy and inexpensive to collect and we would have virtually unlimited information about a species, including population size and trend, vital rates,

movements, and habitat relationships, for single as well as multiple populations. We would be able to use these data in formal models to predict the species' or population's viability and identify factors that are most likely to affect viability. In the real world our knowledge approaches this ideal for only a handful of species. Furthermore, analytic approaches for evaluating population status and viability are often computationally intensive and require some degree of proficiency in statistical modeling. Newer modeling techniques tend not to be represented in currently available, pre-written software packages. The result is a very reasonable reliance on qualitative predictions of management effects on species of concern.

We portray three different levels of data availability typically encountered by biologists. First, and all too often, very little is known about a species beyond basic life history information. This is particularly true for recently listed species or those that are cryptic and difficult to monitor. In this case, detailed analyses of population trends, demographic rates, or metapopulation dynamics are not possible. Alternative, less data-intensive modeling approaches are needed to forecast management effects. In the second level there may be few demographic data available, but abundance estimates have been collected over a period of years. These time series of count data are the product of long-term monitoring programs and are the most common type of existing information for wild populations. Assessing population trend or viability from these data requires fitting appropriate population growth models to the data, and newer methods for doing this are not accessible to many biologists. Finally, there is the optimal situation in which demographic studies have provided detailed information about species vital rates, spatial structure, and metapopulation characteristics. Metapopulation viability analyses are then possible, and newer approaches to sensitivity analysis can tell us which factors most contribute to viability of single or multiple populations. Each of our tools addresses one of these types of data.

PROJECT OBJECTIVE

The overall objective of this program was to develop tools to estimate extinction risk and evaluate management actions for recovery of listed species on DoD-managed lands. The tools were designed to be scientifically based, appropriate for the amount of data available, and easy to use by managers. We provided the theoretical foundation and analytical tools necessary to evaluate the influence of specific management actions on extinction risk. Our approach allowed this evaluation to be made in a rigorous way under a range of levels of biological information, from almost total lack of detailed demographic data where rules-of-thumb must suffice to the ideal where detailed, spatially-explicit estimates of demographic parameters and their variability are available for every population constituting the metapopulation of the species. We developed three tools, each of which was designed to address one of three levels of available data: first, when very little is known about a species, we used life history data to prioritize immediate recovery actions. Second, we used estimates of population abundance over time, the most commonly available type of data, to monitor and project population viability. Third, when there is an abundance of demographic data available for multiple populations, we used metapopulation models to estimate population viability. Together, these approaches allow managers to use the best possible method for assessing the effects of management on population viability and recovery, precluding the need to force different types of data into unsuitable PVA models.

As with any form of population modeling, a constant challenge in estimating population viability is dealing with uncertainty in model predictions. The fourth component of our project involved addressing the issue of uncertainty in predictions of population viability. We developed analytical approaches to quantify overall uncertainty and partition it into contributions from different types of uncertainty including parameter estimation error, error due to model structure, and the links between environmental conditions, human perturbations (such as management or training actions) and parameters of population growth models.

Throughout the project, we demonstrated our approaches using existing, important management issues for focal species on specific DoD installations.

PART 1: GUIDELINES FOR PRIORITIZING MANAGEMENT OF POORLY-STUDIED SPECIES

Background

When a species is under multiple threats, effectively prioritizing management action to achieve recovery is dependent on understanding the role of each threat in depressing overall population viability, and the degree to which those threats can be alleviated through management. Threats can vary in their impact on population viability either because the magnitude of the threats themselves varies, or because they impact different life stages of a species, which in turn contribute differently to population growth. For this reason, understanding how each aspect of a species' life cycle affects its overall population growth is critical to prioritizing management actions. This is particularly true for species that have distinct life stages, often requiring different resources or habitats, leading to a disparate set of threats during each stage of its life cycle.

Demographically explicit population models are extremely useful for identifying the effectiveness of different management options to increase population viability (Morris and Doak 2000, Mills 2007). These models typically use projection matrices, which track changes in the numbers of individuals in different stages (e.g., age or size categories) in a population (Caswell 2001). The stage-specific nature of these models allows researchers to determine whether an increase in any of the species' vital rates, detected by monitoring, actually suffices to reverse population decline. Using these models, researchers can identify factors that most threaten a population, and thus identify particular life stages or demographic processes that should be the primary targets for management (Crouse et al. 1987, Beissinger and Westphal 1998).

The primary drawback of this powerful class of models is their data requirements (Morris et al. 2002). Parameterizing a formal, structured population model is only possible for species for which an abundance of data exists, typically sample means and variances of all demographic vital rates for a population (i.e. stage-specific fecundity and mortality rates). Additional data are required if we want to compare the utility of different management actions in species recovery. For this we also require data on the effect of management in altering each of these vital rates. For the vast majority of threatened and endangered species, these demographic data do not exist (Heppell et al. 2000). Given that such data are often costly, time-consuming and difficult to obtain, management decisions often need to be made before they can be collected (Pullin et al 2004, Bottrill et al. 2009).

Consequently, though we have very powerful tools for conservation, we often lack the data, or the time and resources to collect the data required to link them to actual on-the-ground management. We present here a simple framework based on the principles of structured population models to aid managers in allocating research and data collection efforts, and in clarifying management priorities for such data-poor species. For this approach, we use species-specific life history information to determine the structure of the population projection matrix

that describes the relationship between a species' life cycle and its population growth rate. We then use these life history-specific models to identify which combinations of vital rate values for a particular life history result in positive or negative population growth. In these models, parameter variability can represent environmental stochasticity (process variance), observation error, or a combination of both. As such, by assessing the impacts of increasing levels of variation in any parameter on model output, we can infer which parameters require the most (or least) precision in data collection.

To address the ability of particular management actions to alter species vital rates, we performed a comprehensive review of existing data from previously published management studies, and analyzed these data using meta-analytic techniques. Meta-analysis is a powerful method for synthesizing the results of multiple independent studies to determine the overall effect of some intervention (Gurevitch and Hedges 1993). From each study, an effect size is calculated that quantifies the difference in mean response between treatment and control, standardized by some measure of the size and precision of that study (usually a function of the sample size and standard deviation). As a result, one can calculate the overall magnitude and direction of a treatment effect across studies, as well as the contribution of various covariates to between-study variation in effect size.

Relatively few published studies report quantitative estimates of the impact of management on species vital rates for the taxonomic groups most of conservation interest on DoD installations. Two notable exceptions are the extensive literature describing the impact of various management regimes on bird nest success, and the effects of management measures aimed at reducing competition pressure on plants. We therefore focused our efforts on these data.

First, we analyzed the ability of common management interventions (livestock exclusion, prescribed burning, predator removal programs and cowbird (*Molothrus spp.*) removal programs) to increase avian nest success. Nest predation is the leading cause of reproductive failure in birds (Martin 1995), and for bird species confined to ever shrinking habitat fragments, high rates of nest predation and brood parasitism present immediate threats to long-term persistence (Heske et al. 2001; Ortega et al. 2005). Yet, ultimately, the leading cause of bird declines is the degradation and fragmentation of suitable habitat (Terborg 1989; BirdLife International 2008). Changes in the structure and composition of plant communities that accompany habitat degradation can negatively impact birds by affecting the availability of food resources and suitability of nest sites, both of which may have direct negative impacts on the reproductive success of birds, as well as increasing exposure to predators and brood parasites (Wiens 1973; Johnson and Temple 1990; Saab et al. 1995). Re-establishing historic disturbance regimes through prescribed burning and the manipulation of grazing pressure have increasingly been recognized as an important method for restoring habitat quality (Askins et al. 2000; Brawn et al. 2001). In our analysis of bird management studies, we compared how habitat restoration

measures and parasite and predator control measures affect bird nest success, and determined what variables and conditions lend to the success or failure of these programs.

Our meta-analysis of plant data had two goals: 1) to determine the ability of management actions to increase plant vital rates; and 2) to determine the impact of environmental variability on the effectiveness of this management. Many sensitive plant species are experiencing precipitous population declines due to competitive displacement, and in order to maintain populations of these species, conservation practitioners must manage habitat in a way that minimizes competition (Carlsen et al. 2000; Kaye et al. 2001). Typically, this involves manually removing competitors (e.g. the surrounding vegetation) through weeding and herbicides or by re-introducing disturbance regimes through mowing, grazing and burning. We analyzed the outcome of such competitor removal treatments on three plant vital rates: seedling establishment rate, seedling survival and reproductive output (e.g. the number of flowers, seeds or fruits produced per plant).

The success or failure of any particular management action to increase species' viability can depend on the specific local environmental conditions in which those actions are undertaken. For example, climate has been shown to be a major driver of plant population dynamics (Hobbs and Mooney, 1991, Knapp and Smith, 2001), and any efforts to increase plant population growth rates through management could be helped or hindered by local climate conditions (e.g. rainfall and temperature). While competitor removal programs are carried out with the intent to increase the survival growth and reproduction of target species, some experimental evidence has suggested that the reduction and removal of surrounding vegetation may actually have little or even negative effects on these rates in target species in drought years due to increasing water stress (Ryser 1993; Fischer and Matthies 1998; Eckstein 2005).

Teasing apart the effect of climate variables on the ability of management to increase species vital rates normally requires multiple years of data and thus, the type of long-term studies that managers rarely have the time or resources to undertake. A potential alternative to such long-term studies is to compare the effects of management on species' vital rates across individual studies in the framework of a meta-analysis, with the local climate variables of each study as a covariate to explain variability in management effects across studies. We used this approach to test and compare the ability of climate variables (temperature and precipitation) and ecologically relevant grouping variables (e.g. seed mass, plant longevity, presence of seed bank, conservation status) to mediate the outcome of competitor removal treatments on three plant vital rates: seedling establishment rate, seedling survival and reproductive output.

Methods
Developing life history based demographic models
To determine the relationship between a species' vital rates and its population growth rate, we first determined the timing and duration of each life stage from any available

information on the species' basic life cycle. For example, Figure 1 outlines the life cycle of the arroyo toad (*Bufo californicus*), a federally endangered species located on several military installations in southern California. From the arroyo toad's basic life history information, we can determine which vital rates are necessary to parameterize each transition between every stage of this species' life (Figure 2). With these parameters defined, we can then construct an age-based matrix model that explicitly tracks how the toad's population growth rate varies as a function its vital rates (Figure 3).
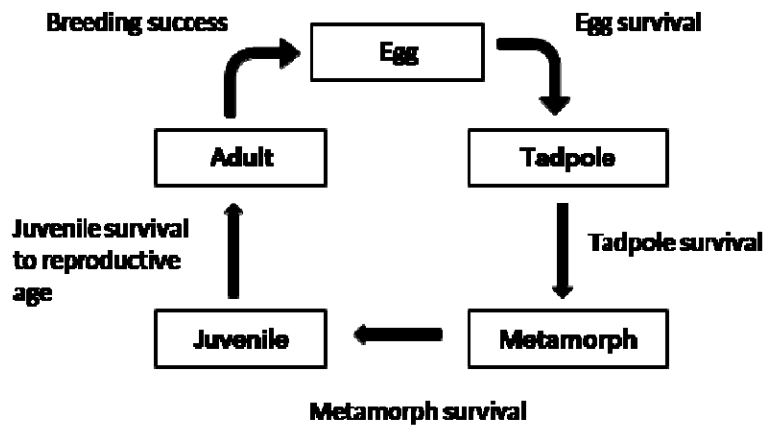
Figure 1: Basic life history information for the arroyo toad (*Bufo californicus).*
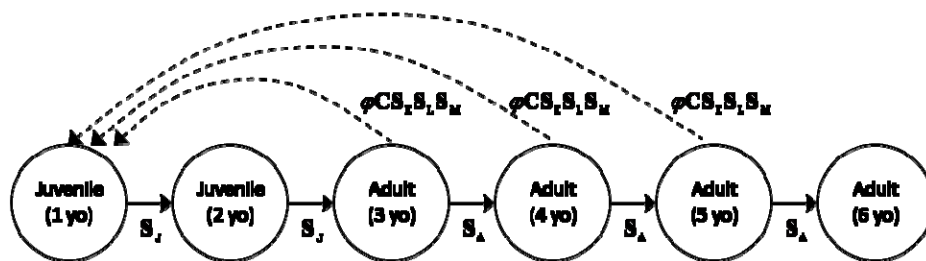
Figure 2: A life cycle diagram for the arroyo toad, showing the combinations of vital rates that make up transitions between age classes. Adults are assumed to senesce at six years.

$$\begin{bmatrix} 0 & 0 & (C\varphi S_E S_L S_M)0.5 & (C\varphi S_E S_L S_M)0.5 & (C\varphi S_E S_L S_M)0.5 & 0 \\ S_J & 0 & 0 & 0 & 0 & 0 \\ 0 & S_J & 0 & 0 & 0 & 0 \\ 0 & 0 & S_A & 0 & 0 & 0 \\ 0 & 0 & 0 & S_A & 0 & 0 \\ 0 & 0 & 0 & 0 & S_A & 0 \end{bmatrix}$$

Figure 3: An age-based projection matrix for the arroyo toad. The model assumed a census of female adult and juvenile toads just prior to breeding (assumed to be synchronous across the population).

To determine the combination of parameter values that result in either positive or negative population growth rate for the arroyo toad, we developed a simple simulation which incrementally increased each parameter between some designated minimum and maximum values (Table 1). Standard matrix analysis techniques (Caswell 2001) were used to calculate the deterministic population growth rate (λ_0) for each possible parameter combination. To quantify the effect of vital rate variability on predictions generated by our general life history models, we used an analytical approach derived from Tuljapurkar's small noise approximation (Tuljapurkar 1982; Haridas and Tuljapurkar 2005). This approach estimates the stochastic population growth rate (λ_S) as:

$$log(\lambda_S) = log(\lambda_0) - \frac{1}{2}\left(\frac{\tau^2}{\lambda_0^2}\right) \tag{1}$$

in which the long-term stochastic population growth rate (λ_S) is equal to the deterministic population growth rate (λ_0), reduced by the effects of vital rate variation:

$$\tau^2 = \sum_{i,j} S_i S_j \sigma_i \sigma_j \rho_{i,j} . \tag{2}$$

where $\rho_{i,j}$ is the correlation between vital rates i and j, and S_i and σ_i are the sensitivity value and standard deviation, respectively, of vital rate i.

For estimations of stochastic lambda, each vital rate is represented by some distribution of values, so in addition to increasing each vital rate mean (μ_i) stepwise from minimum to maximum values, we also specified the amount of variation in each vital rate by altering its standard deviation (σ_i). We altered standard deviations to be either 75% or 25% of the maximum possible value that the appropriate vital rate distribution can take. For example, we represented all survival probabilities as beta distributions (bounded by 0 and 1), while fecundity terms were represented by stretched beta distributions (bounded by some determined biological minimum

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(x_{min}) and maximum (x_{max}) value. The maximum standard deviation allowed for any mean beta value (μ_i) is:

$$\sigma_{i\,max} = \sqrt{\mu_i\left(1-\mu_i\right)} \tag{3}$$

and the maximum standard deviation allowed for any mean stretched beta mean is:

$$\sigma_{i\,max} = \left(\sqrt{\mu_i\left(1-\mu_i\right)}\right)\left(x_{max} - x_{min}\right). \tag{4}$$

Varying multiple parameters simultaneously results in λ values varying in a multi-dimensional space. To present these results in an easy to interpret format, we selected two parameters to vary continuously, while all others parameters vary between some selected "low" or "high" values (Table 1).

We determined which parameter values to use and vary in our models depending on the vital rates most of interest to managers. The arroyo toad has very specific habitat requirements for successful reproduction, and thus a major concern for the maintenance of toad populations has been the effect of alterations to the hydrology of streams used as breeding habitats and the effect these changes have on the probability of toads successfully completing breeding and egg survival (USFWS 1999). Predation of arroyo toads by bullfrogs is another major management concern (affecting all stages, but perhaps larval and metamorph stages are most vulnerable). Other threats listed in its recovery plan are: contamination of breeding streams, degradation of terrestrial habitats and crushing of adults by vehicles. Because management concern focuses mostly on the aquatic stages of this toad, and relatively little is known about its terrestrial stages (i.e. the adult and juvenile stages) we examine how the population growth of this species varies as a function of survival of the terrestrial stages (adults and juveniles), breeding success, and survival of the aquatic stages.

Table 1: Vital rate values used to parameterize the age-structured model for the arroyo toad.

Vital rate description	Symbol	Range used	Values in literature	Reference
Egg survival	S_E	0.5, 0.75	0.55 – 0.84	Blaustein et al. 1994
Tadpole survival	S_L	0.05, 0.2, 0.3	0 – 0.25	FWS Final Recovery Plan (1999)
Metamorph survival (from metamorphosis to 1 year old)	S_M	0.1, 0.3	0.2 0.08	Clark 1977 Biek et al. 2002
annual survival of juvenile toad	S_J	0.5(S_A)	0.26	Biek et al. 2002
annual survival of adult toad	S_A	0.05 – 1.0	0.78	Biek et al. 2002
Breeding success (mean proportion of females laying eggs each year)	φ	0.05 – 1.0	No data	
Clutch size	C	mean = 4,700 (2,000–10,000)	mean = 4,700 (2,000–10,000)	FWS Final Recovery Plan (1999)
Age at reproductive maturity		3 years old	2-3 years old	FWS Final Recovery Plan (1999)
Maximum lifespan		6 years	No data (mean lifespan 5 yrs)	FWS Final Recovery Plan (1999)
Sex ratio		1:1		

This approach described above is best suited for species for which few data are available (e.g. species should be relatively unstudied with regard to demographic information), but that have relatively well-understood life histories. It is not relevant or particularly useful for species which are well-studied, or for which strong ground-truthed management options are already in place. Because we require some information about the basic life history attributes of a species in order to determine how life cycle determines growth rate, we cannot use this approach for species for which basic life history is unknown. Many of the species on DoD installations meeting these criteria share very similar life-history characteristics (e.g. annual plants). Thus, we developed a set of general matrix models and life cycle diagrams for eight distinct life-history types encompassing the majority of these species. These are: annual, perennial and biennial plants, short and long-lived birds, amphibians, small mammals and a turtle. We compiled data on threats and potential management interventions for these groups, and generated model results relating to these threats and actions.

Meta-analyses of management impacts

We conducted our literature searches for studies quantifying the impact of management actions on both bird nest success and plant vital rates using the Web of Science, Agricola, WorldCat and Dissertation Proquest International databases. We supplemented our search from the literature cited sections of retrieved articles and from reviews. We excluded any studies in which multiple management actions were applied together (e.g. managed plots both burned and grazed), studies that compared effects of different management actions without reporting data for unmanaged populations (e.g. burned plots compared to grazed plots), or studies of bird nest success that used artificial nests to estimate nest survival rates.

Many of the studies we retrieved reported data on the effect of a management action for multiple species. For these studies, we considered the results for each species to be independent and calculated effect sizes for each species separately. We considered this appropriate because our primary interest is the response of individual species to management, and how these responses are mediated by each species ecological associations and biological characteristics (Borenstein et al. 2009).

Covariate data and statistical analysis of management impacts on bird nest success

For all studies of management impacts on bird nest success, we collected data on the following covariates to explain between species differences in management effectiveness: 1) study specific variables, such as habitat type and the area of treatment (managed) plots; 2) species specific variables such as the conservation status and the foraging and nesting preferences of target species; and 3) environmental covariates thought to be important within each individual management category, such as measures of grazing intensity, time since fire, and the effectiveness of predator or parasite removals.

We categorized the habitat in which studies were carried out into three main types: woodlands, grasslands and shrub-dominated habitats ("shrublands"). Riparian areas were classified as woodland, and two studies in wetland areas were categorized as grasslands. We specified birds by their nest-layer and foraging guilds, based on species accounts in Birds of North American Online. Nest-layer guilds included ground, shrub-layer and canopy-layer nesting. Foraging guilds included: omnivore, ground insectivore, and above-ground foraging insectivore. The above-ground foraging category combines aerial, foliage-gleaning and bark-gleaning insectivore guilds because of the sparse representation of each these guilds within management categories. We categorized hatchlings as either altricial or precocial.

We specified conservation status of species as either "of conservation concern" or "not of concern." Bird populations were classified as "of conservation concern" if they were: 1) listed as vulnerable, threatened, rare or endangered by the International Union for Conservation of Nature (IUCN) or the U.S. Fish and Wildlife Service (USFWS); 2) identified by the study authors as "declining;" or 3) experiencing significant regional declines (defined as declining trends with p-values < 0.05 from the USFWS Breeding Bird survey trend estimator; Sauer et al. 2008).

We used Hedge's d as our effect size measure, which is the difference in mean nest success between managed plots ($\overline{X}_T$) and unmanaged plots ($\overline{X}_C$) standardized by an estimate of the study's precision and corrected for bias arising from small sample sizes (Hedges and Olkin 1985).

$$\text{Hedge's d} = \frac{\overline{X}_T - \overline{X}_C}{S_p} J \tag{5}$$

where S_p is the pooled standard deviation

$$S_p = \sqrt{\frac{(n_T - 1)s_T^2 + (n_C - 1)s_C^2}{n_T + n_C - 2}} \tag{6}$$

and J is a correction factor for small sample sizes

$$J = 1 - \frac{3}{4(n_T + n_C - 2) - 1} \tag{7}$$

with n_T and n_C representing, respectively, sample sizes for the managed and unmanaged populations, and s_T and s_C the standard deviations of managed and unmanaged populations. The variance of Hedge's d is:

$$v = \frac{n_C + n_T}{n_C n_T} + \frac{d^2}{2(n_C + n_T)} J^2. \tag{8}$$

Hedge's d can be interpreted as the difference between mean nest success in managed and unmanaged plots measured in units of standard deviations. Thus, an effect size of 0.8 indicates that, on average, nest success is 0.8 standard deviations greater in managed plots than unmanaged plots. Effect size values less than zero indicate decreased nest success with management.

We first tested for differences in effect size means from the full set of bird species in each management category (livestock exclusion, prescribed burns, predator removal programs and cowbird removal programs), then tested how only those species considered to be of conservation concern differed in their responses to these interventions. We conducted each analysis as a random-effects weighted analysis of variance (ANOVA). We considered a random-effects model to be most appropriate for our analyses because we assumed that there is real, unexplained variation in effect sizes between studies that cannot be accounted for by our chosen grouping variables (Borenstein et al. 2009). In each analysis, study effect sizes (Hedge's d; eqn. 5) were weighted by the inverse of their variance (eqn. 8) (Hedges and Olkin 1985). Analyses were carried out in Metawin 2.1 (Rosenberg et al. 2000).

We tested the ability of our selected covariates to explain heterogeneity in effect size between species within each management category using a random effects multiple regression approach. This approach partitions the total variation across species effect sizes into estimates of within-species variation and between-species variation, and then estimates how well covariates explain the latter (Higgens et al. 2003). For each management category, we started with a model that included all covariates for which we had complete coverage across studies (see Appendix A, Supporting Data, for data on covariates), then simplified these models using backwards stepwise selection to eliminate covariates with non-significant effects. We then separately tested the effect of covariates that were available only for a subset of studies, again simplifying models through a backwards stepwise process. All analyses were carried out using the module Metareg in STATA (version 11; STATA Corporation, College Station, Texas) (Sharp 1998).

Covariate data and statistical analysis of management impacts on plant demographic rates

For our analysis of the impact of competitor removal treatments on plant demographic rates, we included the following covariates: habitat type, characteristics of the focal species (life form, longevity, seed mass, presence of a seed bank and conservation status), climatic data (precipitation and temperature) specific to the location and timing of the study, and whether soil disturbance was included in the competitor removal treatment.

The vast majority of studies identified by our literature search took place in grasslands. Study authors classified these habitats as oligotrophic, mesic, semi-arid or Mediterranean. We used these same habitat categories in our analysis, with the exception that we combined semi-arid and Mediterranean habitats into one category given that these systems both tend to be shaped by strong inter-annual variability in water availability (Levine and Rees 2004).

If authors did not provide ecological characteristics of their study species, we obtained these data from outside sources (seed mass from: Kew Botanical Gardens seed database [Liu et al. 2008]; presence of seed bank: Thompson et al. 1997). In addition, we classified all species as either "of conservation concern" or "not of concern." Plants were classified as "of conservation concern" if they were listed as vulnerable, threatened, rare or endangered by either IUCN or USFWS or identified by the study authors as "declining."

In order to compare the effect of competitor removals on vital values that can differ by several orders of magnitude (e.g. proportion of seeds emerging versus seed set per plant), we required an effect size that could provide a relative measure of change with management. We chose the response ratio (R):

$$R = \frac{X_T}{X_C} \tag{9}$$

in which X_T and X_C are the mean demographic rates of a species in managed plots and unmanaged plots, respectively (Hedges et al. 1999). We used the natural log of the response ratio (ln(R)) in our analyses to meet assumptions of normality, but report results in units of R (eqn. 9).

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In meta-analyses, study effect sizes are typically weighted by some estimate of study precision. In parametric meta-analyses, this precision is usually quantified as the inverse of within-study variance, a function of standard deviation and sample size. Variation of the response ratio is given as:

$$V_{ln(R)} = \frac{(S_T)^2}{n_T X_T} + \frac{(S_C)^2}{n_C X_C}$$ (10)

in which S_T, S_C, n_C and n_T are, respectively, the standard deviations and the number of replicates for control and treatment plots (Normand 1999). Because a number of our studies did not report standard deviations nor the information to calculate them, we chose instead to use a non-parametric measure of study precision (V_{np}) based on sample sizes alone (Adams et al. 1997):

$$V_{np} = \frac{(n_C + n_T)}{n_C n_T} .$$ (11)

First, we tested for differences between habitat types in the effect of management on each rate as a random-effects weighted analysis of variance (ANOVA). In each analysis, study effect sizes (eqn. 9) were weighted by the inverse of their non-parametric variance estimate (eqn.11). Our use of non-parametric estimates of study variance precluded the use of parametric statistics to calculate p-values. Thus, p-values were calculated using a bootstrap procedure (Adams et al, 1997). Analyses were carried out in Metawin 2.1 (Rosenberg et al. 2000). Studies concerning the effect of competitor removals on fecundity rates only included one species in oligotrophic habitats, so this habitat category was dropped in our analysis of fecundity rates.

We then tested the ability of our selected covariates to explain between-species heterogeneity in effect size for each vital rate in each habitat type using a random effects multiple regression approach. For subsets of vital rate data from species in each habitat category, we started with a model that included all covariates, then simplified these models using backwards stepwise selection to eliminate covariates with non-significant effects. Analyses were carried out using the module Metareg in STATA (version 11; STATA Corporation, College Station, Texas) (Sharp 1998). P-values were calculated through permutation tests to account for our use of non-parametric variance estimates ("permute" option in STATA; Higgens et al. 1999).

Determining the effect of climatic variability on management effects

To incorporate the effects of climatic variability into our analysis, we obtained climate data from a number of climate databases (US and global: NOAA National Climatic Data Center; Europe: Koninklijk Nedelands Meteorologisch Instituut; Canada: National Climate Data and Information Archive; UK: MetOffice; Australia: Bureau of Meteorology; New Zealand: National Institute of Water and Atmospheric Research). For each study, we identified the weather station closest to the study site, and the appropriate time frame for the development of each life stage based on the experimental census periods and life history information. For each month of the appropriate time period, we obtained data on both the deviation from average precipitation (DPNP in mm) and deviation from average temperature (DPNT in degrees Celsius), and

calculated study-specific seasonal average of both. Because extreme precipitation events may also have an effect on experimental outcomes that might be obscured by averaging, we also recorded the DPNP of the driest and wettest months for each study. We used deviations from average precipitation and temperature as our climate variables so that we could compare across regions that experience very different climate conditions (as opposed to absolute temperature or precipitation values).

Temperature and precipitation are often correlated, so we tested for significant correlations before including these two parameter types in our analysis. In semi-arid habitats, temperature and precipitation variables were significantly correlated ($P = 0.019$, $r^2 = -0.506$), and so we included only precipitation variables when analyzing data from these habitats. In mesic and oligotrophic habitats, we found no correlation between temperature and precipitation ($P = 0.074$, $r^2 = 0.398$ and $P = 0.692$, $r^2 = -0.14$), and so included both variables in our models. Likewise, because our three precipitation variables (seasonal average, wettest month, driest month) were interdependent, we tested each variable in a univariate analysis, then picked the best one (highest R^2) to be in our full model. Of the three precipitation variables, the mean seasonal DPNP demonstrated the best explanatory power in mesic habitats. In oligotrophic and semi-arid habitats, the DPNP of the driest and wettest month, respectively, demonstrated the best explanatory power.

Results and Discussion
Life history modeling

Results from our deterministic model for the arroyo toad demonstrate that population growth rate is strongly influenced by adult and juvenile survival (Figure 4). The steep slope of the curves in Figure 4 indicate that even small changes in these rates can have a large impact on its long term population persistence. When tadpole survival is low (20%; Figure 4a), the population will always decline if annual adult survival drops below 62%, even if all females successfully breed and lay eggs every year. However, if the survival of the toad's terrestrial stages (the adult and juvenile stages) is very high, it can endure relatively low rates of breeding success, with the minimum threshold for positive population growth at 19% of females successfully breeding each year. Even a small increase in tadpole survival can lead to a relatively more optimistic picture: when tadpole survival is increased from 20% to 30% (Figure 4b), the toad population could persist with adult survival rates as low as 45% at 100% breeding success.
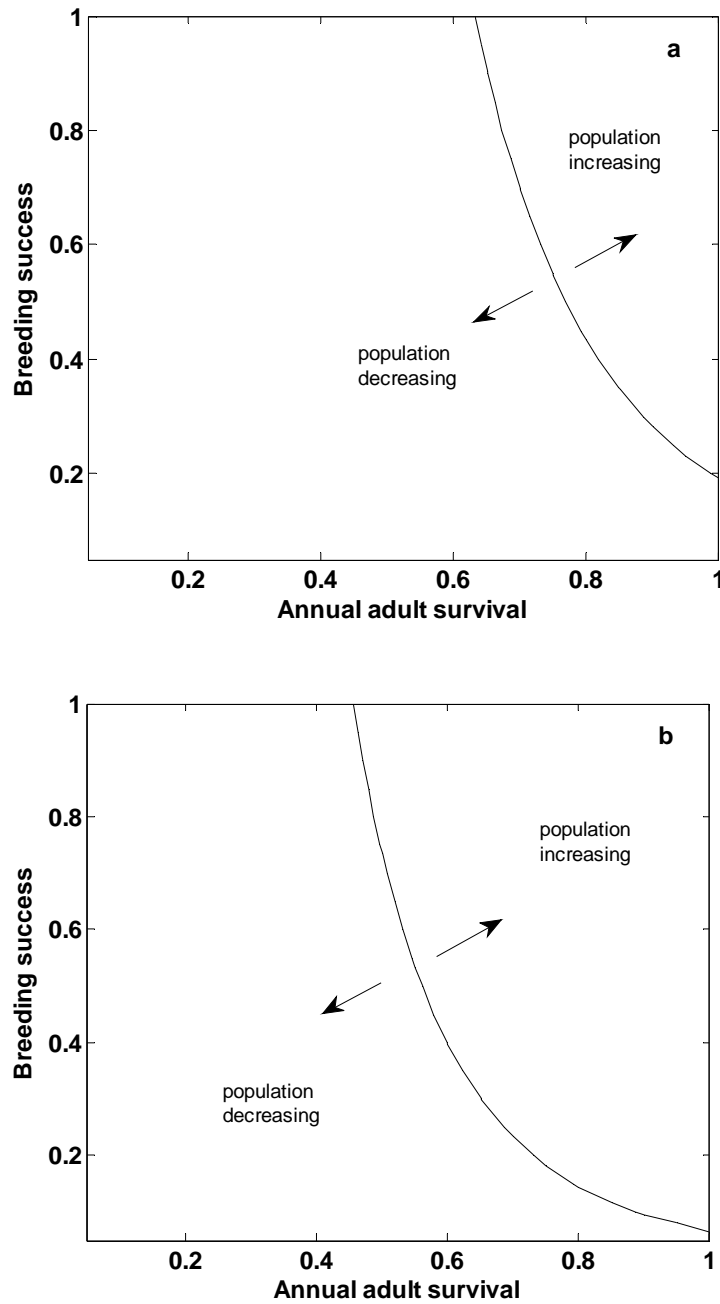
Figure 4: The relative contribution of breeding success (the probability a female successfully finds a mate and lays eggs in any given year) and the annual survival rate of adult and juvenile toads on population growth rate. Areas to the right of each curve represent parameter combinations that lead to positive population growth rate ($\lambda > 1$), and to the left, population declines ($\lambda < 1$). In plot (a) tadpole survival is 0.2 and metamorph survival is 0.1; in (b) tadpole survival is 0.3 and metamorph survival is 0.1. Juvenile survival is set to be half that of adults.

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These results illustrate the importance of identifying and alleviating mortality factors in the arroyo toad's terrestrial stages. Except during the breeding period, the arroyo toad is thought to be essentially terrestrial (USFWS 1999), and as such, the survival of adult and juvenile toads may depend on the availability of adequate terrestrial habitats. Our results highlight the importance of identifying these terrestrial resource needs and the factors that might be negatively impacting them. In addition, our results suggest that even sources of juvenile and adult mortality that are seemingly minor, such as crushing by vehicles, could potentially have large impacts on population growth rate.

Including variability in all vital rates so that they vary at 25% of their maximum possible standard deviation (σ) values (eqn. 3 and 4) greatly reduces the parameter space of positive population growth for the arroyo toad (Figure 5). However, an additional increase in the variability of breeding success and egg survival to 75% of their maximum possible values has little additional effect on population growth. In contrast, increasing just the variability of survival rates for the aquatic stages of this toad (larval and metamorph survival) to 75% of their maximum values always results in population declines (no parameter combinations of adult survival and breeding success lead to positive growth). This highlights the importance of accurately estimating survival of the aquatic stages of the arroyo toad, and the strong sensitivity of population performance estimates to errors in the estimation of these parameters.
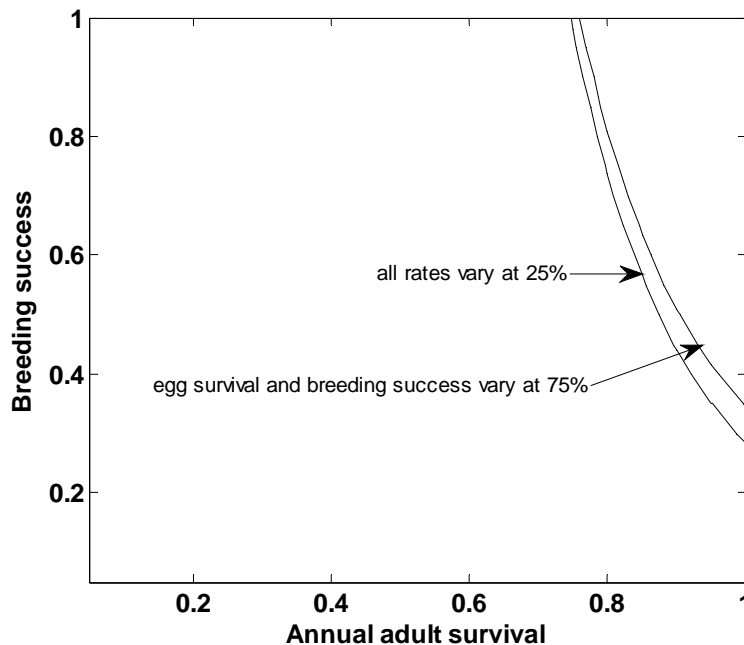
Figure 5: Stochastic model results for arroyo toad. Parameter values are the same as in Figure 4, but now all vital rates vary with the σ of each vital rate set at 25% of its maximum value, or with the σ of egg survival and breeding success set at 75% of its maximum value (and all others at 25%). Setting the σ of larval and metamorph survival at 75% of its maximum value always results in population declines, and thus is not shown.

Effects of management actions on avian nest success

   Results from our meta-analysis of bird nest success indicated that all management interventions increase nest success on average, with predator removal programs resulting in the greatest increase (P = 0.045; Figure 6). Nest success was approximately 1.2 standard deviations greater in plots with predator removal than in non-removal plots, whereas controlled burns, livestock exclusion and cowbird removals resulted in nest success increases 0.52, 0.46 and 0.75 standard deviations greater than their respective controls. Results from livestock exclusion studies were by far the most variable, with the 95% CI intervals overlapping zero. In contrast, results from just the subset of species considered to be of conservation concern indicated that livestock exclusion produced the largest increase in bird nest success, though high variation led to low statistical power (P = 0.55). On average, nest success was approximately 1.3 standard deviations greater in livestock exclusion plots for these species, while controlled burns, cowbird removals and predator removals resulted in nest success increases 0.66, 0.84 and 1.2 standard deviations greater than their respective controls.
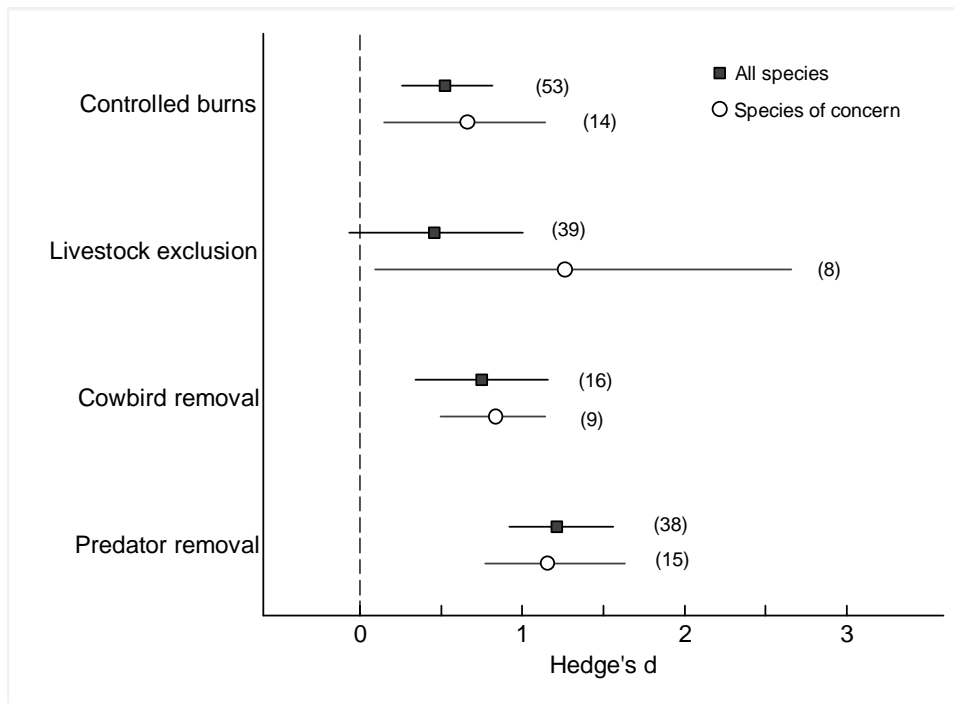
Figure 6: The mean effect of the four management interventions reviewed for both the full set of bird species, and for only species considered to be of conservation concern. Hedge's d is the difference in nest success between managed and unmanaged plots, standardized by the size and precision of each study. Values greater than zero mean the management action increases nest success, values less than zero indicate a decrease in nest success under management. The number of species is in parentheses. Error bars represent 95% bootstrapped confidence intervals.

Of the four management interventions analyzed, our chosen covariates were only able to significantly explain variation in species' responses to controlled burning. In particular, when all other covariates were controlled for, increases in nest success between burned and unburned plots increased with the amount of time elapsed since the burn ($P = 0.03$), and species in shrub dominated and woodland habitats demonstrated significantly smaller increases in nest success than those in grasslands ($P = 0.047$ and 0.01, respectively). Regarding the generality of the positive trend in nest success with increasing time since fire, an important caveat to consider is that grassland birds appeared to gain the greatest benefits from burning, and most of these species experienced annual burns. In our analysis, we excluded several studies in grassland systems that examined longer fire-return intervals because they lacked unburned controls, or combined burning treatments with grazing treatments. As a consequence, the increased benefit with increased time since fire indicated by our results should not be extrapolated to grassland systems.

While all four of the management interventions reviewed increased bird nest success on average, predator removal programs were by far the best option for increasing nest success when both common species and species of conservation concern were considered together, with an average increase more than twice that of the other treatments. However, when we considered the effects of these management actions on only threatened, endangered or declining species, we found that livestock exclusion resulted in the largest average increase in nest success. Thus, for some species of concern, habitat restoration measures can be just as, and possibly more effective than, predator and parasite control.

Results from livestock exclusions were far more variable than those of the other treatments, and our analysis indicated that much of this effect size heterogeneity was due to differences in the responses of individual species to this management action. While none of the covariates we tested were statistically able to explain this variation, some noteworthy patterns emerged. As noted above, the most striking pattern is the large increase in nest success experienced, on average, by species of conservation concern when grazers were excluded from their nesting habitat. In contrast, more common species only exhibited a relatively small (and non-significant) increase in nest success.

In order to make comparisons across management types we focused our analysis on bird nest success. As such, we run the risk of underestimating the true effects of brood parasite (cowbird) removal programs, the main impact of which should be on host recruitment rates. However, we found that cowbird removals resulted in nest success approximately 0.75 standard deviation units higher than in non-removal sites, lending support to the idea that in addition to reducing parasitism rates, cowbird control also decreases overall abandonment and nest predation rates (Zanette et al. 2007). Unfortunately, the relatively small number of studies documenting the effects of cowbird removals makes it difficult to make robust inference from such results, highlighting the necessity of these types of studies. While the existing literature on the effects of cowbirds on their hosts is extensive (e.g. Lorenzana and Sealy 1999), the results of

our literature search indicate that studies documenting the actual effect of cowbird management on host populations remain relatively rare.

Overall, our results suggest that all four management actions can be beneficial in increasing bird nest success, and that, in some cases, habitat restoration measures can be as or more effective at increasing nest success as direct control of predators and brood parasites. We focused on nest success in this study because this demographic rate is by far the most widely studied and reported for bird species (Faaborg et al. 2010), and is considered to be a good indicator of habitat quality (Pidgeon et al. 2006). However, the ultimate importance of nest success to the population growth rate of any one bird species will depend on that species' individual life history (Saether and Bakke 2000). Yet while the importance of collecting more comprehensive demographic data (both reproduction and survival rates) in association with manipulative management studies has been widely recognized (e.g. Sherry and Holmes 1995, Donovan et al. 2002, Fletcher et al. 2006), studies doing so remain rare.

Effect of competitor removals on plant demographic rates
The effect of competitor removals on seedling establishment and seedling survival differed significantly across habitats (Figure 7; $P < 0.001$ and $P = 0.005$ respectively), with species in oligotrophic habitats experiencing the largest increases as a result of management. While there was considerable variation in the results of management on species in oligotrophic habitats, these results were consistently positive. In contrast, the 95% CI of the mean effect size of competitor removal treatments on seedling survival and reproductive output in semi-arid/Mediterranean habitats overlapped zero, indicating that this management action does not always to lead to increased rates for target species in these habitats. The effect of management on fecundity measures did not significantly differ between mesic and semi-arid habitats ($P = 0.07$).
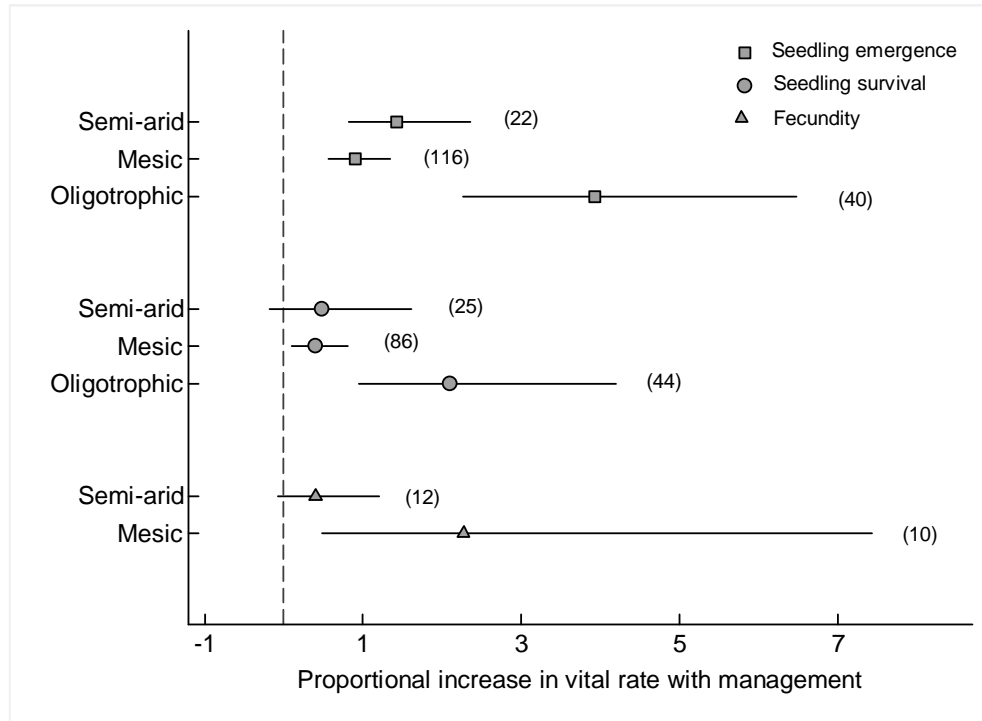
Figure 7: Mean increases in seedling establishment, seedling survival and fecundity of various plant species after the implementation of management to decrease resource competition, partitioned by habitat type. Values greater than 0 indicate an increase in the vital rate with management. Error bars denote 95% bootstrap confidence intervals. Values in parentheses are the number of species studied.

Determining the effect of climatic variability on management effects

Our analysis of the covariates determining the direction and magnitude of the effects of competitor removals on plant vital rates within each habitat type indicated that the effect of climate on management also varied between plant life stage and habitat types. Precipitation levels had no discernable influence on the effect of competitor removals on seedling establishment rates in semi-arid habitats, only the conservation status of the target species significantly explained variation in effect size across species ($P = 0.046$). In contrast, in mesic and oligotrophic habitats, both precipitation and temperature significantly explained differences in management effects on seedling establishment rates across species. In mesic habitats, the effect of management on seed germination rates was significantly greater for species with persistent seed banks ($P = 0.001$) and increased as a function of increasing mean seasonal precipitation and decreasing mean seasonal temperature ($P = 0.041$ and $P = 0.006$, respectively; Figure 8). There was no significant interaction between presence of a seed bank and climate variables. In oligotrophic habitats, effect size increased as a function of decreasing precipitation

(DPNP of driest month) and with decreasing seed size (P < 0.001 and P = 0.007, respectively; Figure 9).

In contrast, our analysis of management effects on seedling survival rates revealed almost the opposite trend as that found for seedling establishment. Precipitation significantly explained differences in results from studies of competitor removals on seedling survival rates in semi-arid habitats (P = 0.001; Figure 10). Regressing seedling survival against the DPNP of the wettest month occurring during the seedling growth period in each study, we found that management is most effective at increasing seedling survival during growing seasons without intervals of high precipitation (e.g. no months experience greater than average rainfall). In contrast, none of our covariates significantly explained variation in the effect of management on seedling survival in mesic and oligotrophic habitats.

Climate variables had no statistically discernable effect on the ability of management to increase the reproductive output of target plants. This result may be due to the smaller sample sizes of studies quantifying management effects on plant fecundity measures.
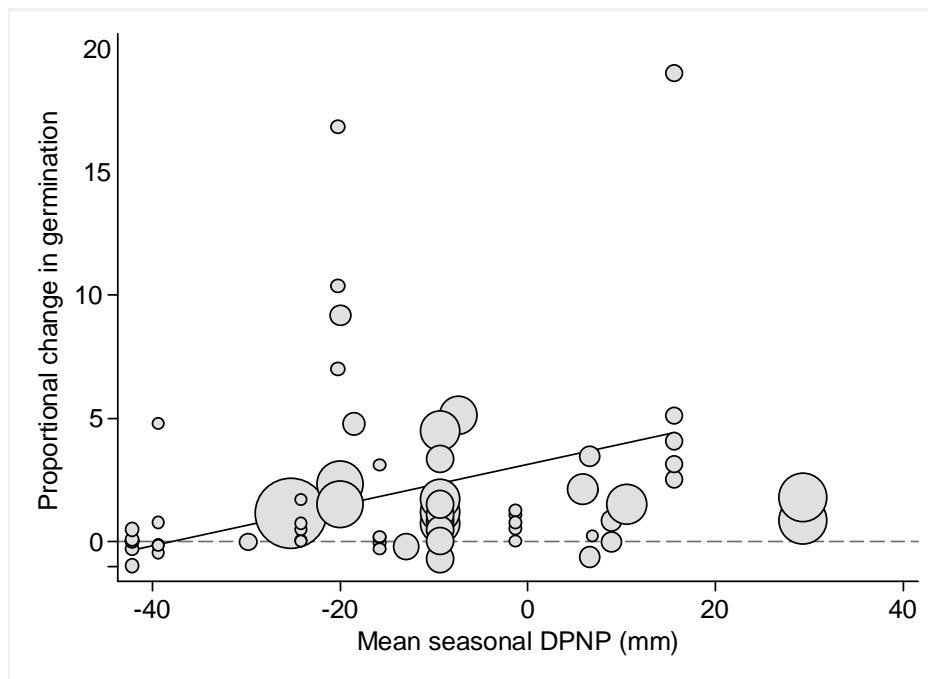
Figure 8: In mesic grasslands, the ability of management to increase seedling establishment rates significantly increases with increasing mean seasonal precipitation (slope = 0.018; P = 0.04). DPNP is mean departure from normal precipitation. Marker size indicates the relative weight of study results, a function of study sample size.
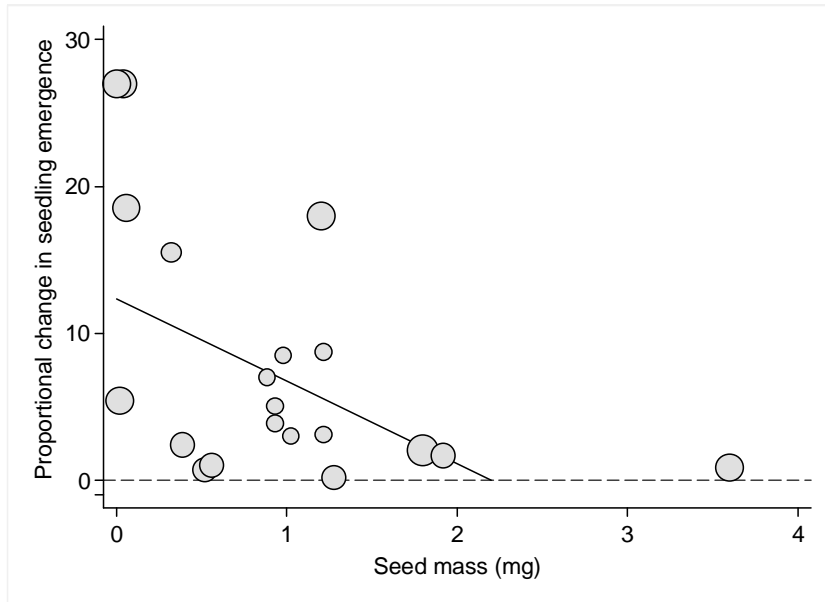
Figure 9: In oligotrophic grasslands, the ability of management to increase seedling emergence rates decreased significantly with increasing mean seed mass of the target species (slope = -0.71; P = 0.007). Marker size indicates the relative weight of study results, a function of study sample size.
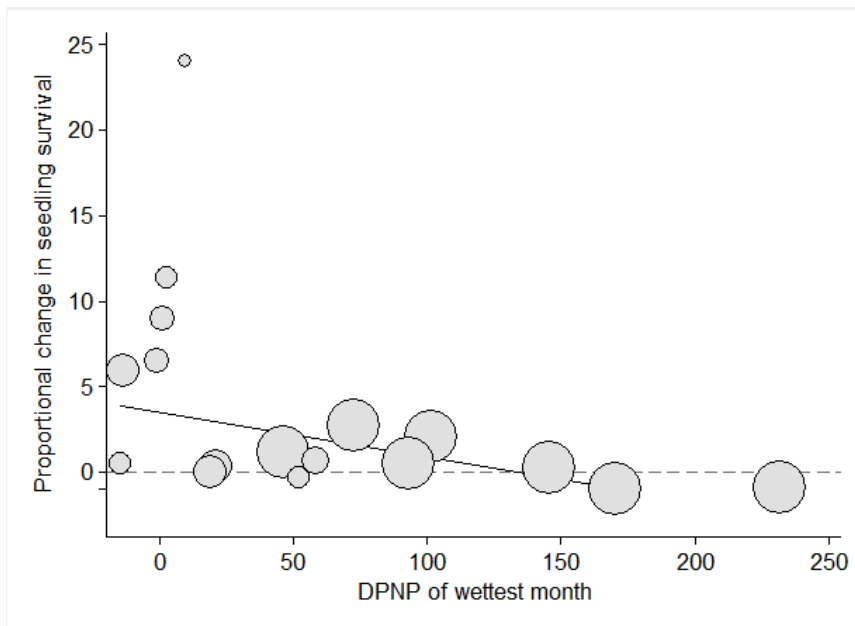
Figure 10: In semi-arid grasslands, the ability of management to increase seedling survival rates significantly decreased in very wet growing seasons (slope = -0.025; P = 0.001). DPNP is mean departure from normal precipitation. Marker size indicates the relative weight of study results, a function of study sample size.

Our results indicate that climate variables can have a strong influence on the ability of management to increase plant vital rates, but that these effects vary between the vital rate measured and the habitat in which the study took place. In oligotrophic and mesic habitats, precipitation and precipitation and temperature together influenced seedling establishment rates respectively, yet neither of these variables could significantly explain variation in seedling survival rates in these habitats. In contrast, in semi-arid habitats, precipitation had no consistent influence on seedling establishment, yet was the only significant covariate explaining variation in seedling survival rates. Most notable, in semi-arid habitats, our results indicate that if competitor removals are undertaken in growing seasons with very high precipitation levels, this management effort has no effect on, and sometimes even decreases, seedling survival.

Why might high precipitation lead to decreased management effectiveness in semi-arid habitats? One answer may be that in rainy seasons, surrounding vegetation recovers more quickly from management, resulting in similar vegetation cover in control and treatment plots and little overall reduction in competitive pressure on target plants (e.g. Holl and Hayes 2006). More perplexing is the result that in very rainy years, management actions may actually decrease seedling survival of target plants. It has previously been shown that cutting and subsequent re-growth can result in stronger resource depletion by the re-sprouting vegetation (Silvertown et al. 1992, Edwards and Crawley 1999). Therefore, cutting surrounding vegetation to decrease competition on some target plant in very rainy conditions, which allow for rapid re-growth of the cut vegetation, may paradoxically lead to stronger competition pressures exerted on the target plant.

Our results indicate that competitor removal treatments in oligotrophic habitats lead to the greatest increases in both seedling establishment and seedling survival rates, though these results were also the most variable. This result is largely a consequence of the very low germination rates in this habitat in the absence of management. Our results also emphatically confirm the oft reported result that competition has a stronger inhibitive influence on establishment of small seeds than larger (e.g. Coomes and Grubb 2003), as our results suggest a significant increase in the effect of competitor removals with decreasing seed size. Precipitation also strongly influenced this between species variation, with studies taking place in drier than average years leading to increased effectiveness. Again, this result may be a consequence of slower re-growth of the clipped/removed vegetation in drier seasons, giving the target species more time to establish before competition sets in.

Our effect size choice may have influenced the results of our meta-analysis of management effects on plant vital rates. As a measure of proportional increase, the response ratio inflates very small absolute increases. Using another effect size, such as Hedge's d, that measures the absolute difference between vital rates in control and treatment (Hedges and Olkin 1985), could very well lead to different conclusions. However, we considered the response ratio to be the most appropriate effect size measure for comparing management effects because it provides a measure of relative increase across vital rates: we are comparing the effect of

management across vital rates which differ vastly in their values. Both seedling establishment and seedling survival are probabilities that range from zero to one, yet establishment values tend to be extremely small (e.g. 0.005), whereas seedling survival tends to be much higher (e.g. 0.2), while seed set values can be in the thousands. In order to compare the effects of management actions on these different values, we needed a relative measure of effect.

Do these results give us any useful information for more effective management of plant populations? Our clearest results concern species in semi-arid and oligotrophic habitats, in which management is most effective at increasing vital rates in drier years and less effective in wetter years. Seasons with drier conditions should inhibit growth of many exotic grasses, a major source of resource competition for plant species of concern in these environments. These results suggest that an efficient management approach may be to postpone management efforts in wetter years, or to apply management with more effort (e.g. mowing or weeding more often) to inhibit re-growth of problematic vegetation. Our results also re-emphasize the importance of placing the outcome of any management action in its specific context, including local climate conditions, and in quantifying management effects in more than one year before determining if management is having its desired effect. By understanding how environmental variation alters the effects of management actions, either by negating or enhancing these effects, we may be able to determine guidelines for what environmental conditions should be take into account when developing and implementing ecological research and management plans.

Management of Chorro Creek bog thistle, Camp San Luis Obispo

The Chorro Creek bog thistle (*Cirsium fontinale* var. *obispoense*) is a federally endangered species restricted to San Luis Obispo County, California. One of the largest populations occurs at Camp San Luis Obispo. In November 2010, we met with managers from Camp Roberts, Camp San Luis Obispo and Fort Hunter Liggett to discuss the use of generalized population models to prioritize management actions and data collection efforts for the bog thistle (henceforth: CCBT). In particular, managers have been concerned with understanding the importance of cattle trampling/grazing, seed predators and inter-specific competition as potential threats to the long term population viability of this species, as well as identifying and exploring potential management actions they could undertake to ensure CCBT's persistence.

We developed a basic life history model for CCBT (see Appendix A for the life history diagram and model) and determined how population growth is predicted to change as a function of the vital rates associated with management concerns. The vital rates of concern include the probability of a seed surviving to germinate (seed predation), the probability of successful seedling establishment (inter-specific competition) and the survival of adult plants (trampling and browsing by cattle). Seedling establishment rates in plants are often extremely variable, dependent on climatic conditions to cue germination and allow seedlings to establish, and as on microsite and seed availability (Harper 1977). Thus we were particularly interested in how variability in seedling establishment rates would affect our model output.

Survival of adult CCBT (from the seedling stage to flowering) is typically quite high (greater than 60%; David Magney Environmental Consulting 2006), and results from our deterministic model suggest that the population can persist with seedling establishment rates less than 10% (Figure 11a). Our deterministic model results also suggest that population growth rate is relatively insensitive to changes in seed survival rates (from 40% to 10% plotted in Figure 9). However, when we include high variability (75% of the maximum possible standard deviation) in seedling establishment rates, we see the parameter space for positive population growth shrinks drastically. Now seedling establishment rate must be much higher (at least greater than 15%) for populations to persist and small changes in seed survival rates result in large differences in potential growth rate (Figure 11b).

Seedling establishment rates tend to be very low in many plant species, and are considered a bottleneck for plant population growth (Harper 1977, Grubb 1977). Our model results indicate that with strong environmental variation, CCBT would need to achieve relatively high seedling establishment rates for long term persistence. In the USFWS 5-year status review of the Chorro creek bog thistle, understanding the potential impacts of intra-specific competition on this species was specifically singled out as a topic in need of further investigation (USFWS 1998). We discussed the design for a manipulative seed sowing experiment, which would allow managers to determine both seedling establishment rates and the effect of competitive interactions from surrounding vegetation on this rate. We also discussed potential for a collaborative effort in which data from these field experiments could be coupled with our modeling efforts in an adaptive management framework to quantitatively determine the impact of potential management actions (such as the re-introduction of grazing) to achieve long term stability and recovery for this species.
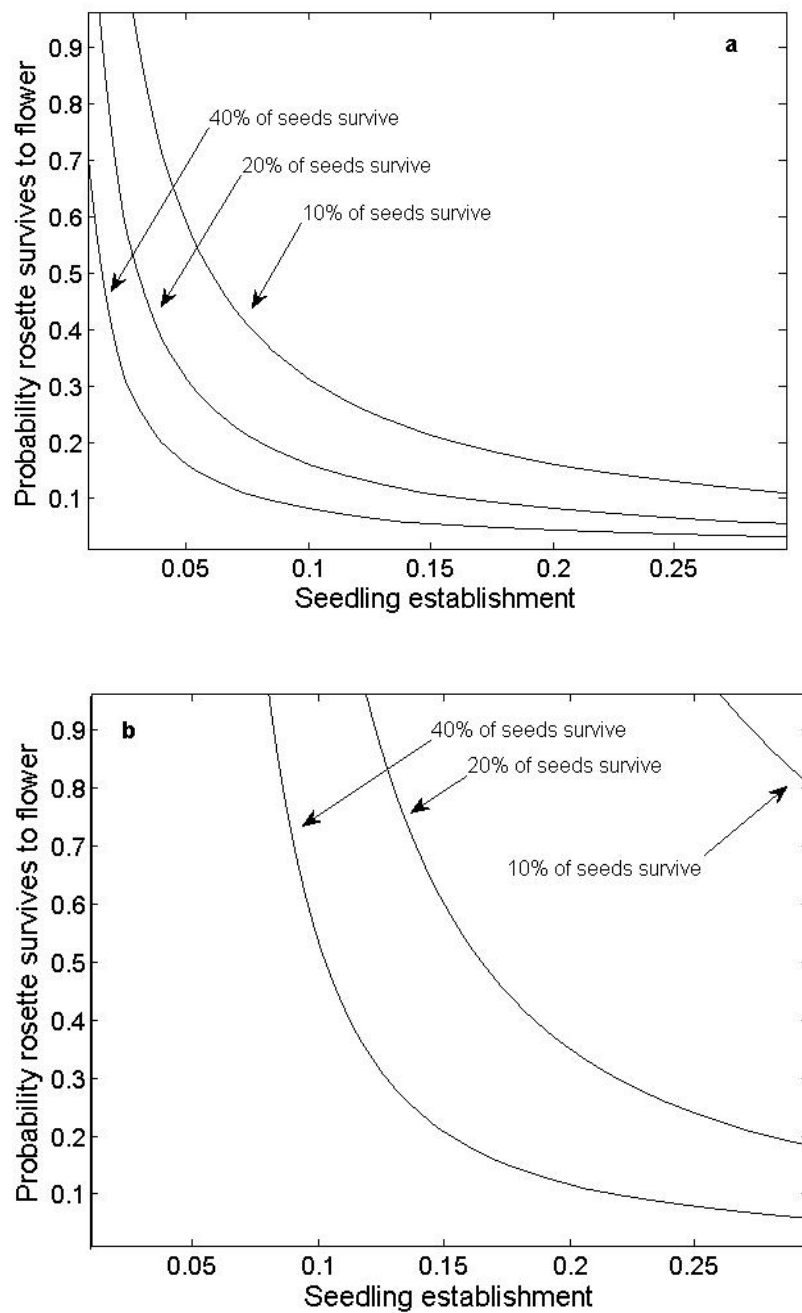
Figure 11: The relative contribution of adult survival (to flowering), seed survival, and the probability that a germinating seed successfully establishes on the Chorro Creek bog thistle's population growth rate, as predicted by a deterministic (a) and stochastic model (b). As in Figure 4, areas to the right of each curve represent parameter combinations that lead to positive population growth rate ($\lambda > 1$). Each curve represents a different probability of a seed surviving to germinate.

PART 2: INTERPRETING ABUNDANCE DATA: TIME-SERIES POPULATION VIABILITY ANALYSIS

Background

An accurate assessment of endangered species population trend and future viability is essential to sound management decisions. In some cases a positive trend is a criterion for downlisting or delisting a species; in others, a declining trend triggers specific management or recovery actions. Implementation of a monitoring program is a core recovery action for most species (Neel et al. in prep) and provides the basis for assessment of a population's risk of extinction.

One of the most common types of empirical data resulting from monitoring programs is a time series of abundance. These data can be complete counts where every individual in the population is censused or, more commonly, abundance is estimated using established methods or indexed where a constant proportion of individuals in the population are counted. All of these data types are suitable for fitting stochastic models of population growth, several of which have been developed to include things like the observation error associated with abundance estimates, stochastic processes related to environmental conditions that cause populations to fluctuate randomly through time, density dependence in which intra-specific competition affects growth rates, and, most importantly, environmental covariates that can be tied to management actions.

Population trend, or change in population abundance over a period of time, can be quantified from parameter estimates of these population growth models. Stochastic growth models can take into account the influence of sampling error or process (environmental or demographic) variance and can be used to quantify the effect of environmental or management-related factors on population growth. These models can be further categorized as exponential growth models, in which changes in population abundance are unaffected by the density of organisms in the population, or as density-dependent models in which a population's density influences its growth rate. Accurate assessment of population trend is absolutely dependent on using the correct model (exponential growth models with or without sampling error and process noise, or density-dependent growth models) to describe growth for a particular population. Choosing the correct model also affects our ability to accurately predict future abundance or persistence of the population.

Methods

Modeling population growth and trend

We can use time series of population abundance to answer fundamental questions about the status and viability of a population. What is the "trend"? Is the population increasing, decreasing, or stationary? What is its probability of persistence into a period of time in the future? Is there density dependence in annual growth rates? How do environmental conditions affect population growth rates? Being able to quantify population trend and how it is influenced

by density dependence or external factors allows us to form effective management strategies to stabilize or recover endangered species.

Estimation of population trend can be used for two primary purposes: first, to quantify trend for its own sake (e.g., is my population of concern increasing or decreasing?), and second, for incorporating into PVA models. For the second purpose, we fit population growth models to abundance data collected over time. After fitting the models, parameter estimates from the most appropriate model can be used to predict future population trajectories and estimate the probability of persistence under different management scenarios or environmental conditions. A discussion of all the models used to estimate population growth can (and does) fill textbooks (see Morris and Doak 2002 and Mills 2007). Here we'll briefly describe six specific models that incorporate stochasticity. The first three are density independent models. The remaining population growth models are density dependent and are presented assuming discrete and equally-spaced sampling times.

1. Exponential growth with observation error (EGOE): This model assumes that variability in the data arises purely from the imprecision of abundance estimates (observation or sampling error), with the population itself governed by deterministic exponential growth. The model for deterministic exponential growth takes the form

$$\ln\left(n_t\right) = \ln\left(n_0\right) + \mu t$$

where n_t = abundance at time t and μ is the trend parameter which can be interpreted as the expected difference in log-abundances separated by one time unit.

Now let $x(t) = \ln(n_t)$ be the true log abundance at time t and $Y(t)$ be the estimated or observed log abundance. The stochastic model for $Y(t)$ is

$$Y\left(t\right) = x\left(t\right) + F$$

where, on the log scale, F is normally distributed observation error with mean = 0 and variance = τ^2 written as $F \sim normal\left(0, \tau^2\right)$.

2. Exponential growth with process noise (EGPN): This model assumes the population abundances through time are measured without error but that deviations from deterministic growth arise from environmental stochasticity causing random fluctuations in population growth rate (i.e., process noise; Dennis et al. 1991, Lande et al. 2003). Thus, the stochastic model for changes in log abundance from time t to time $t + dt$ is

$$d(X_t) = \mu dt + dB_t$$

where $dB_t \sim normal(0, \sigma^2 dt)$

3. Exponential growth with process noise and observation error (EGSS): This model has been called the exponential growth state-space model (Dennis et al. 2006, Holmes 2001, Staples et al. 2004) and assumes that variability in abundances results from both sources of variation (observation error and process noise). Thus, the EGSS model can be written as a combination of the EGPN and EGOE models.

$$d(X_t) = \mu dt + dB_t \qquad \text{stochastic process governing actual abundances}$$

$$Y_t = X_t + F \qquad \text{stochastic process governing observed or estimated abundances}$$

4. Ricker: This model assumes that changes in log abundance are a decreasing, linear function of population size (i.e., growth rate is depressed as the population gets larger).

$$\ln(N_{t+1} / N_t) = a + bN_t + E$$

where a = maximum growth rate at $N = 0$ (i.e., *Rmax*) and b = effect of intraspecific competition; and $E \sim normal(0, \sigma^2)$

5. Gompertz: The Gompertz growth model is similar to the Ricker model except that growth rate is a decreasing, linear function of the *natural logarithm* of population size.

$$\ln(N_{t+1} / N_t) = a + b \times \ln(N_t) + E$$

6. Theta-logistic: Again, the theta-logistic growth model is similar to the Ricker model except that in this case, growth rate is a decreasing, linear function of population size *raised to the power theta (θ)*.

$$\ln\left(N_{t+1} / N_t\right) = a + bN^\theta_t + E$$

Unfortunately, fitting some of these models can be numerically intensive, and to date there have been no pre-written software programs that can fit and provide parameter estimates for all of the models described above. Managers and applied ecologists have not been able to take advantage of new techniques effectively. To remedy this problem, we have developed user-friendly software called PopGrowth to perform the calculations necessary for parameter estimation for each of the models.

PopGrowth is intended for use by natural resource managers who wish to evaluate population trend or persistence using monitoring data. PopGrowth is a program written to facilitate estimation of relevant parameters of stochastic population growth models based on time-series of abundance data. After estimating model parameters, these estimates can be used to infer population trend or predict future viability of the population. The program is written in Visual Basic 6, which provides a "front-end" user-friendly interface. When running PopGrowth, the free statistical computing software R (http://cran.r-project.org/) and R contributed package PopGrowth4 is used for many of the calculations. This is done in the background and users do not need to be familiar with R to use PopGrowth. A PopGrowth installation guide and tutorial is included as Appendix C.

Time-series of abundance data can be imported from Excel spreadsheets or text files. The user can then select several stochastic growth models to fit to the data. PopGrowth output provides a printout of the input data, parameter estimates for each model, model residuals and model selection criteria (e.g., Akaike's Information Criterion, AIC).

Parameter estimates from population growth models provide not only the means to quantify population trend but also to calculate metrics that describe extinction risk (e.g., mean time to extinction, probability of falling below a population threshold). Once we have obtained parameter estimates, we can enter them into a simulation program such as MetaPVA (described in "Managing Multiple Populations" section below) to calculate the population size in one year time steps into the future, starting with the current population size. The simulation program repeats this calculation hundreds of times, accounting for environmental variation, to produce estimated probabilities of extinction risk.

For three population growth models (EGPE, Ricker and Gompertz), PopGrowth calculates model residuals. These can be used to identify correlations among populations in a metapopulation or investigate possible influences of environmental covariates on growth rates.

As emphasized above, selection of the most appropriate model is essential to accurately projecting population growth or persistence. PopGrowth calculates AIC for four models (EGPE, Ricker, Gompertz, and theta-logistic) to provide an information-theoretic basis for evaluating which model is best supported by the data.

PopGrowth also includes an option for "Viable Population Monitoring" (VPM; Staples et al. 2004). A recent development in the conservation biology literature, VPM is a risk-based monitoring strategy that seeks to monitor the viability of a population through time instead of monitoring the population abundances and relying on estimates of trend. It offers greater power to detect "problems" with the population's viability than relying on statistical measures of a "significant" trend (Staples et al. 2004). PopGrowth provides an easy way to implement VPM for annual evaluation of risk.

Dealing with unequal time intervals when modeling population growth and trend

Missing data in time series observations of population abundances are a recurring and frustrating problem. Many statistical models for ecological time series data, especially those incorporating realistic population dynamics, require observations spaced at equal time intervals. Ecological sampling however involves constraints of time, personnel, and budgets and do not always live up to the designs and requirements of statistical models. As well, ecological systems that have intrinsically continuous-time dynamics, such as some aquatic systems, are sometimes sampled at unequal time intervals. The data that exist in studies with missing data or unequal time intervals are potentially informative, and precluding such data from analysis could affect conclusions regarding the biological resources in question. Ecology could benefit from having better models for accommodating time series data with unequal time intervals.

Recently Dennis et al. (2006) described a "state-space" population model for use in ecological time series analysis. The model, termed the Gompertz state space (GSS) model, represents one of the simplest possible formulations containing density dependence, stochastic process variability, as well as stochastic observation or measurement error. The simplicity of the model allows for an explicit likelihood function and for parameter estimation through ordinary numerical maximization. State space population models of greater complexity require simulation-intensive computer algorithms for fitting (de Valpine and Hastings 2002, de Valpine 2002, 2004, Clark and Bjornstad 2004, Ionides et al. 2006, Lele et al. 2007, Ponciano et al. 2009). Unfortunately, the GSS model as described by Dennis et al. (2006) does not accommodate observations collected at unequal time intervals, as caused for example by missing data or by survey design.

A special case of the GSS model is a density independent state space model. The exponential growth state space (EGSS) model was introduced by Holmes (2001), and parameter estimation was studied by Lindley (2003) and Staples et al. (2004). The EGSS model has been generalized to apply to unequal time intervals (Staudenmayer and Buonaccorsi 2006, Humbert et al. 2009).

We have extended the full density dependent GSS model to unequal time intervals. The method used is to employ a continuous-time diffusion process model, the Ornstein-Uhlenbeck process, for population abundance on the logarithmic scale. The resulting state space model has discrete-time statistical properties identical to those of a GSS model. The generalization makes accessible a parametric bootstrap likelihood ratio test of density independence versus density dependence for time series abundance data with missing observations. An R program for fitting the model to data is provided in Appendix C.

Results and Discussion: Evaluating Persistence of Greater Sage-Grouse, Yakima Training Center

Greater sage-grouse (*Centrocercus urophasianus*; sage-grouse, hereafter) have declined in both numbers and distribution throughout most of the western United States and now occur on less than 60% of their pre-settlement range (Schroeder et al. 2004). UFWS is currently reviewing the status of sage-grouse range-wide to determine whether listing under the Endangered Species Act is warranted (USFWS 2008). With 47 DoD installations falling within the current sage-grouse range, DoD recognizes the need to actively manage the species and its sagebrush habitat to stabilize or increase sage-grouse populations across its range (DoD and USFWS 2007).

The species' decline is particularly pronounced in Washington, where it occupies only about 8% of its historical range in the state (Stinson et al. 2004). The sage-grouse was listed as a threatened species by the state of Washington in 1998 and a recovery plan for Washington was released in 2004 (Stinson et al. 2004). A population of less than 400 birds is found in contiguous shrub-steppe on Yakima Training Center (YTC), an Army training facility. As one of two primary populations of sage-grouse in Washington (Figure 12), the YTC population is critical to persistence of sage-grouse in Washington.

Natural resource managers at YTC are charged with helping to meet the state's recovery goal of 3,200 sage-grouse state-wide. Through seasonal restrictions on training near sage-grouse leks, an intensive monitoring program, and habitat restoration, YTC's sage-grouse management plan seeks to reverse the species' decline on Army lands. Managers are interested in determining the efficacy of ongoing protection and restoration measures in increasing sage-grouse persistence, both at YTC and for the Washington population as a whole. Specifically, managers posed the following questions:

1. Under current training and management programs, what is the probability of persistence of the YTC population over 30 and 100 years?

2. For leks with the greatest amount of protection, how does each contribute to persistence of the YTC population?

We provided information to answer these questions to fit population growth models and estimate the probability of extinction under different scenarios specific to each management question.
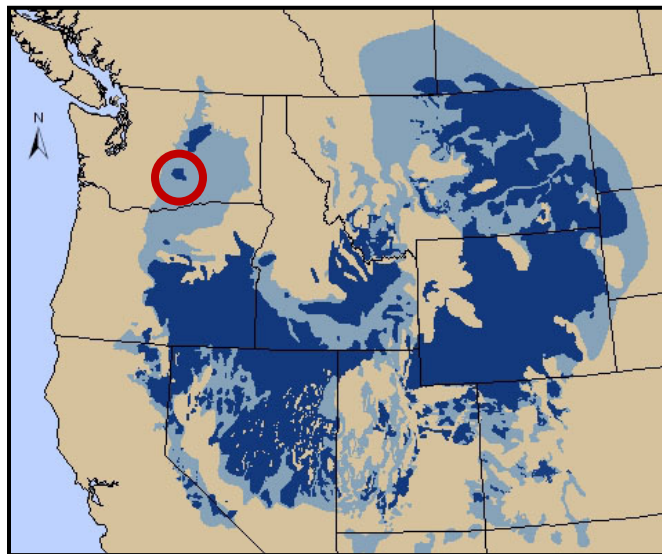
Figure 12. Historical range (light blue) and current distribution (dark blue) of greater sage-grouse in western North America. Red circle highlights the location of the Yakima population of sage-grouse, Yakima and Kittitas Counties, Washington.

Analytical Approach

Sage-grouse lek counts have been conducted at a few leks at YTC since 1970, but in 1989 YTC biologists began extensive counts that included more leks and more systematic monitoring. Efforts increased again around 2002, when multiple counts began at each lek during each breeding season (YTC 2008). Today YTC continues to conduct one of the most intensive sage-grouse monitoring programs available. In the long-term dataset, however, there remain data gaps for years in which not all leks were counted. To address this problem and develop a long-term dataset for trend analysis, we used existing lek counts to reconstruct an index for historical abundances of the population (see Garton and Horne *in press*).

In earlier work, we used the program PopGrowth to fit a series of population growth models to sage-grouse lek count data collected between 1972 and 2006. With abundance data only (i.e., no environmental covariates), we found that there was no single "best" model to describe population growth. Because competing models provided different parameter estimates, there was too much uncertainty in population projections using those estimates to be reliable. To reduce uncertainty, we next incorporated environmental covariates to estimate the amount of

model error that could be attributed to environmental stochasticity and density dependence. We used an object-oriented analysis of historical LANDSAT satellite images of the Yakima area to develop maps of major land cover types in 1972, 1982, 1992, and 2006. From these maps we estimated the amount of each cover type at YTC for every year between 1972 and 2006, interpolating within intervals to obtain annual estimates. We obtained climate data for each year to evaluate the influence of temperature, precipitation, drought, and snow on sage-grouse population growth. Using this dataset (Table 2) we fit a series of exponential and density-dependent population growth models to sage-grouse lek counts from 1972-2006. We used an information-theoretic approach (Burnham and Anderson 1998) and Akaike's Information Criterion for small sample sizes (AICc) to evaluate the plausibility of each model.

Table 2. Environmental covariates included in population growth models for sage-grouse at Yakima Training Center, Washington, 1972-2006.

Covariate	Description
Sage	Area of sage shrublands (km^2)
Grass	Area of grasslands (km^2)
Mean Temperature (MT)	Mean monthly temperature (^{o}F), March-May
Mean Precipitation (MP)	Mean monthly precipitation (in), March-May
Departure from Normal Temperature (DNT)	Mean departure from normal monthly temperature (^{o}F), March-May
Departure from Normal Precipitation (DNP)	Mean departure from normal monthly precipitation (in), March-May
Snow	Maximum snow depth (in), December-March
PDSI	Palmer Drought Severity Index score
Hours<4C	Number of hours with temperatures < 4°C, October-March

Once the best model had been identified, we used the model parameter estimates to simulate future population growth using the R code included in Appendix C (*R Code: Fitting population growth models and projecting future Sonoran pronghorn viability*), modified for our dataset. We predicted the probability of reaching an extinction threshold of fewer than 50 males

at 30 years in the future. When the best model included an environmental covariate, we held that covariate constant at current levels for future projections. For example, we assumed that the amount of grassland cover in the area will not substantially change from current levels in the next 30 years.

To evaluate the relative importance of individual leks to the persistence of the YTC population, we estimated the probability of extinction of the YTC population for four scenarios: the existing situation in which all leks remain active, and three scenarios in which individual leks with strong protection measures are lost. We modified our dataset to sequentially remove population estimates and amount of habitat for each of the leks with highest levels of protection (Lmumma, Range 5, and Range 10Z leks). We fit the best population growth model for the YTC population, which included a habitat covariate, then used its parameter estimates to project probability of extinction for YTC sage-grouse under each scenario. For this analysis we included population abundance data from 1989-2006 because not all leks were monitored prior to 1989.

Findings

Reconstructed estimates of population abundance (represented by minimum number of males at leks) showed an overall declining trend from 1972-2006 (Figure 13).
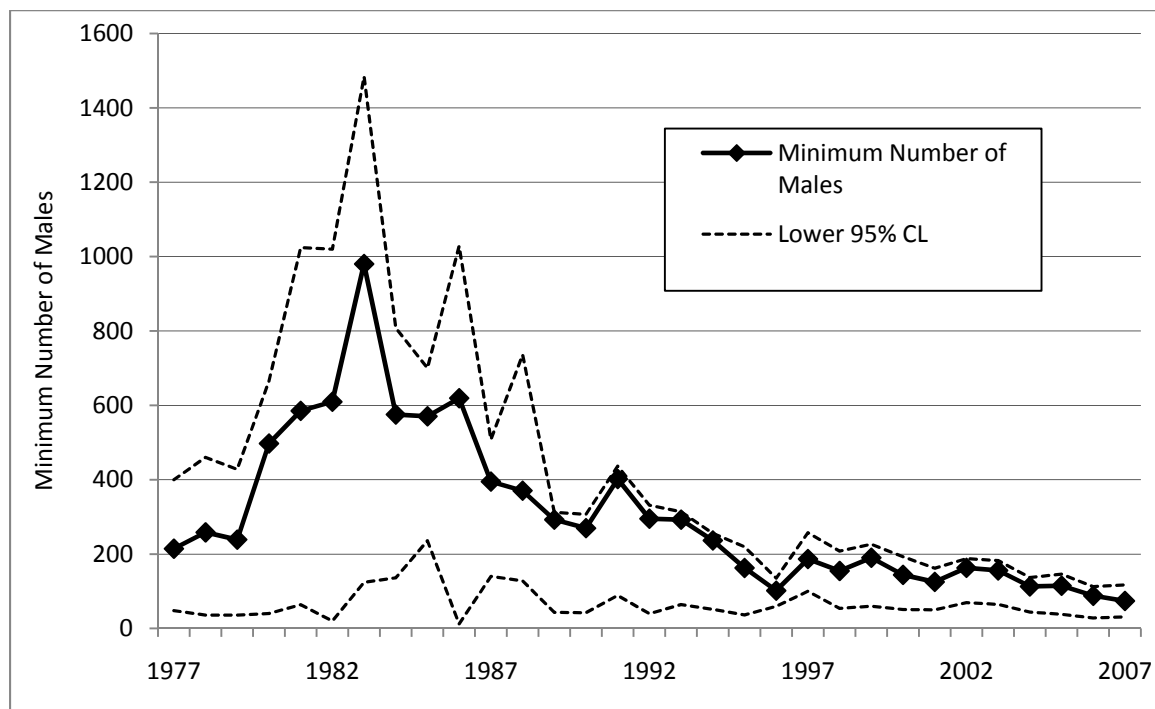
Figure 13. Reconstructed population estimate for Yakima Training Center greater sage-grouse, 1972-2006.

There was little evidence for density dependence in the YTC sage-grouse population (Figure 14). Exponential population growth models were better supported than those incorporating density dependence (Table 3). The 2 best-supported models were exponential growth with area of grassland cover and exponential growth with Palmer Drought Severity Index score.
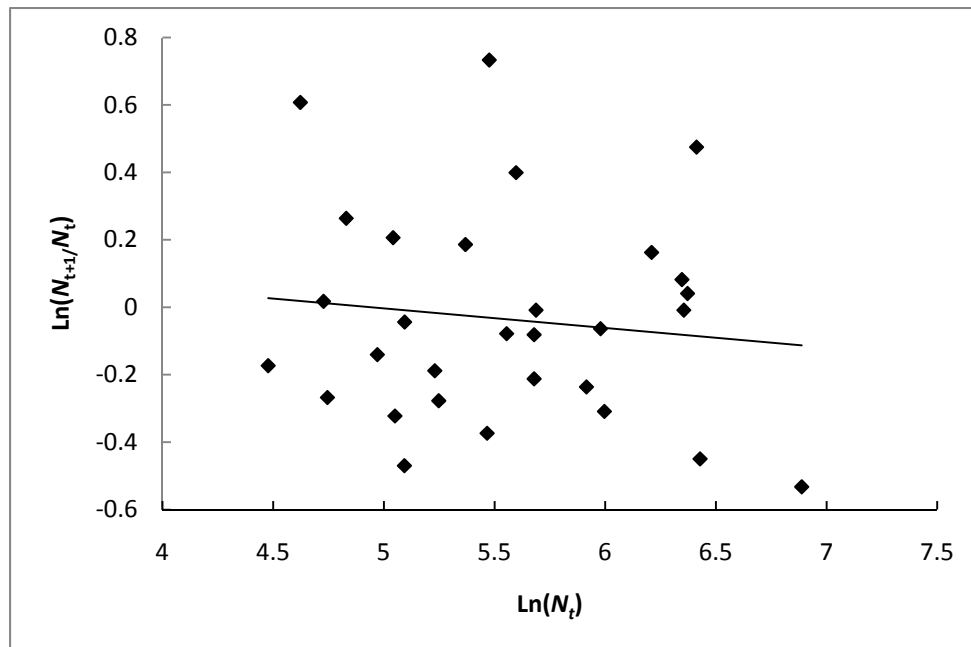
Figure 14. Pattern of density dependence in the Yakima Training Center greater sage-grouse population 1972-2006.

Population projections using parameter estimates from these models yielded similar probabilities of persistence. Overall, the probability of the YTC population reaching an extinction threshold of less than 50 lekking males within 30 years was 82% under the model with grassland area (Figure 15) and 75% under the model with drought index. The probability of the YTC population getting above 100 lekking males within 30 years was 9% and 12%, respectively.

Table 3. Candidate set of exponential and density-dependent population growth models with environmental covariates.   Models were evaluated based on Akaike's information criterion corrected for small sample size (AIC$_c$). K is the number of estimable parameters in the model, ΔAIC$_c$ is the difference in AIC$_c$ between the current model and the best model, and w_i is the Akaike weight indicating relative support for the model. Twenty population growth models were considered, and those with negligible support (ΔAIC$_c > 6$) are not listed. Environmental covariates are described in Table 2.

Model	Model Statistic		
	K	ΔAIC$_c$	w_i
EGPE + Grass	3	0.0	0.28
EGPE + PDSI	3	0.1	0.27
EGPE + Snow	3	2.4	0.08
EGPE + Sage	3	2.5	0.08
Gompertz + Grass	4	4.1	0.04
EGPE + Snow, Hours<4C	4	4.2	0.03
EGPE + Sage, Grass	4	4.6	0.03
Gompertz + PDSI	4	4.9	0.02
EGPE + DNT, DNP	4	5.4	0.02
Gompertz + Snow	4	5.4	0.02
EGPE + MT, MP	4	5.5	0.02
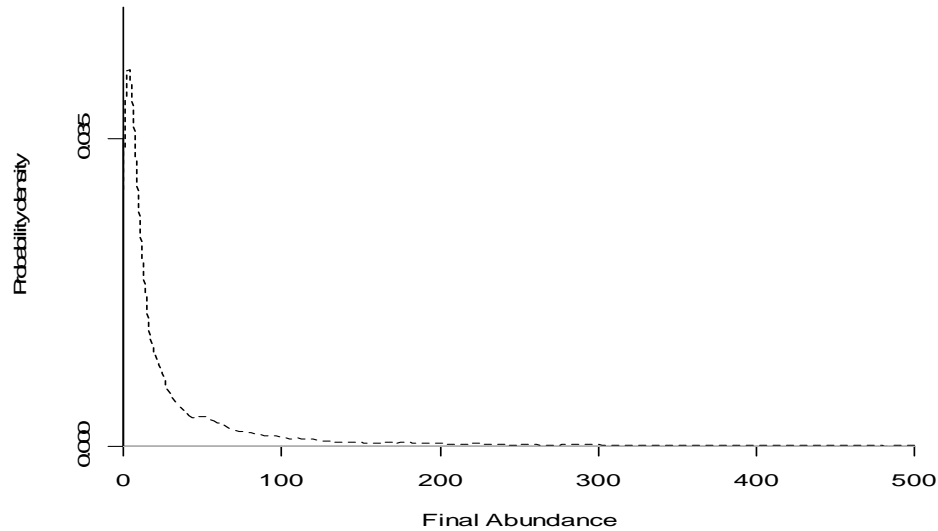
Figure 15. Probability density of final abundance of sage-grouse 30 years in the future based on exponential growth models that included area of grass-dominated communities as a covariate.

Extinction probabilities under the exponential growth model with grass as a covariate indicate that the probability of the YTC population falling below 50 males within 30 years is greatest if either the Lmumma or Range 10Z leks are lost (Figure 16).
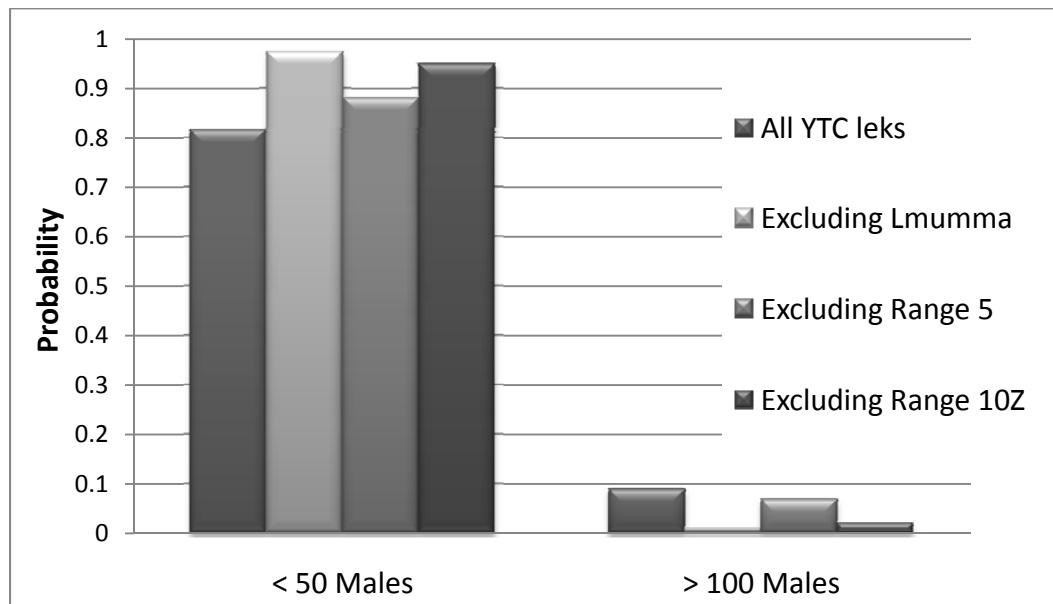
Figure 16.   Relative contribution to YTC population persistence of active leks with the greatest protective measures.   Probability within 30 years of YTC sage-grouse population a) falling below 50 lekking males or b) exceeding 100 lekking males.

Implications

Historically, YTC was dominated by sagebrush shrublands with very little grass cover. Our habitat classification showed grasslands increasing dramatically during the 34 year period (Figure 17), mostly likely due to a combination of development and wildfires that convert shrublands to grasslands dominated by non-native grasses such as cheatgrass (*Bromus tectorum*). Because population growth rates in YTC sage-grouse were negatively correlated with area of grassland (Figure 18), our results underscore the importance of preventing wildfires and protecting native shrublands from development in designing management programs to averting further declines in sage-grouse populations. Managers at YTC can use this information to design and implement appropriate protection measures for sage-grouse leks, nesting, brood-rearing, and wintering areas.   Population growth rates were positively correlated with drought severity scores (Figure 19), suggesting that population growth is greater in years with more soil moisture and precipitation. Although drought and other climate variables are beyond the control of military managers, these results have implications for the persistence of sage-grouse as climate change is predicted to alter precipitation and temperature patterns in the Columbia Basin.
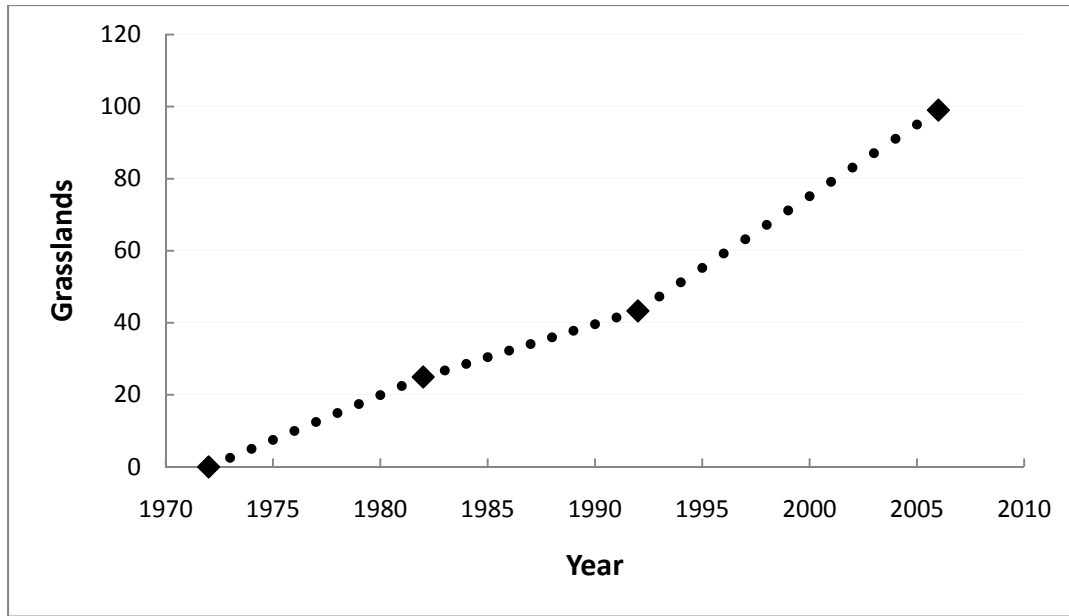
Figure 17. Changes in area of grass-dominated communities (km^2) in and near Yakima Training Range, Washington, 1972-2006. Values for 1972, 1982, 1992, and 2006 (diamonds) were estimated from object-oriented classification of LANDSAT images from those years. All other years (circles) were interpolated using the assumption of a constant annual change within each interval.
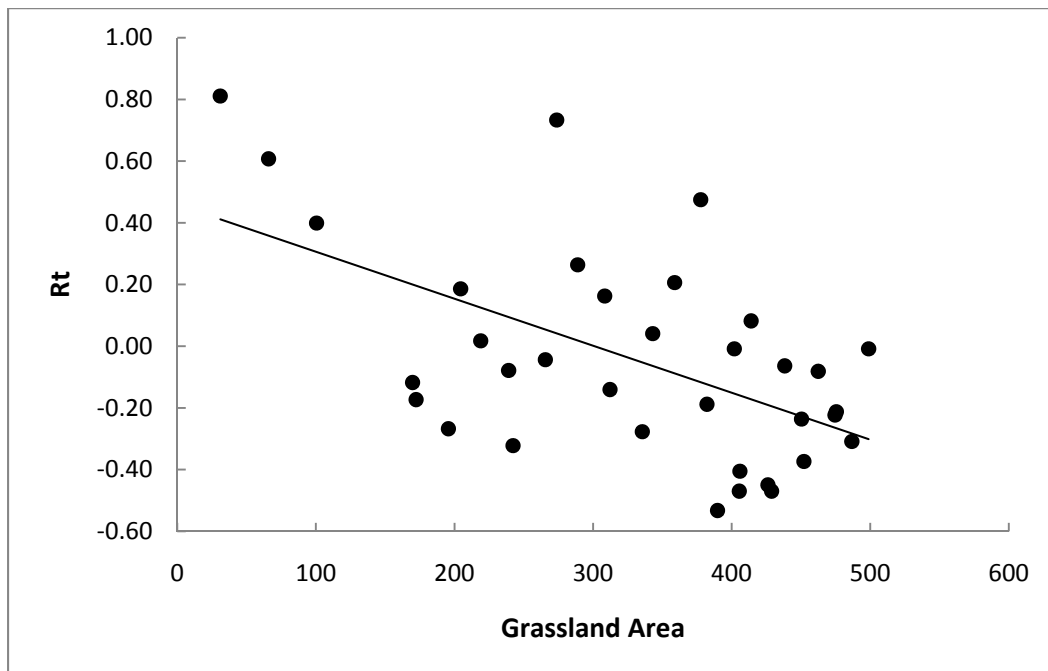
Figure 18. Relationship between area of grass-dominated communities (km^2) and population growth rate for the Yakima sage-grouse population, 1972-2006.
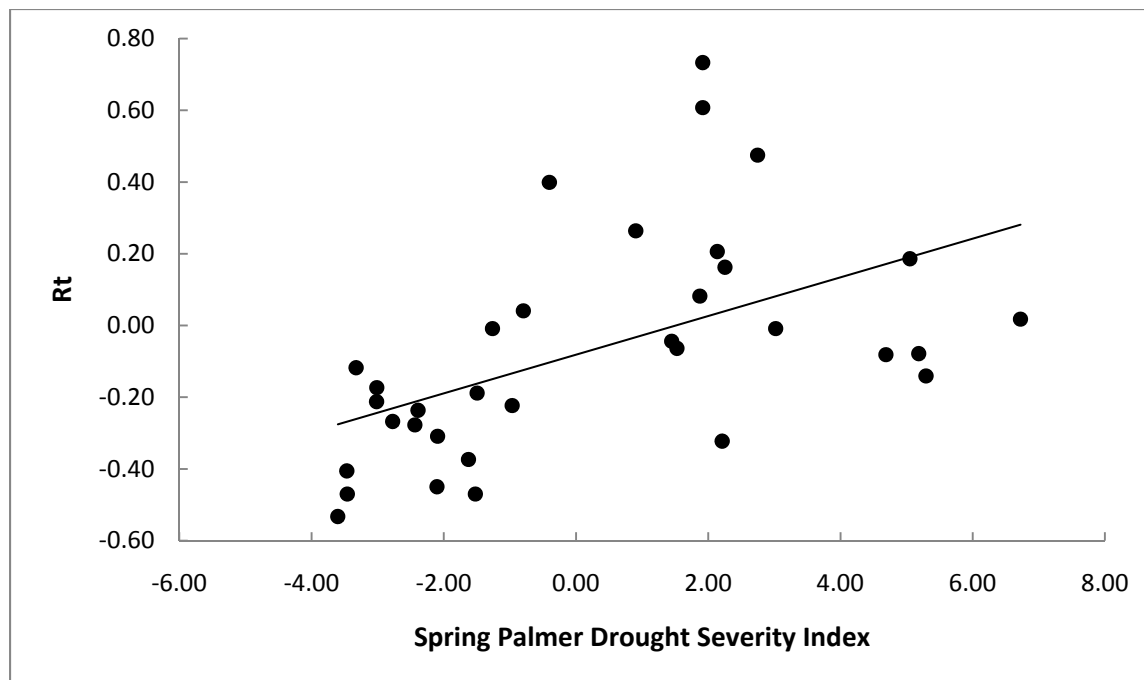
Figure 19. Relationship between average spring (March-May) Palmer Drought Severity Index score and population growth rate for the Yakima sage-grouse population, 1972-2006. Negative PDI scores indicate drought conditions.

PART 3: MANAGING MULTIPLE POPULATIONS: SENSITIVITY ANALYSIS OF METAPOPULATION MODELS

Background

The fact that many listed species occur in spatially sub-divided populations (i.e., a metapopulation) suggests that, when sufficient data exist for parameterization, a viability model capable of capturing metapopulation processes and structures will offer the greatest flexibility for determining the effects of management actions on species' viability. Furthermore, endangered species occupying military installations usually represent only a fraction of the entire population. Therefore, when evaluating the effects of management and/or training on DoD installations, there is often the need to determine the relative effect of site-specific management/training actions on overall persistence and how these effects change under varying assumptions of metapopulation structures and processes. Because of the significance of this question for management of listed species occupying military installations, we initiated research to develop the necessary methods and tools for quantifying the importance, in terms of species viability, of various components (e.g., characteristics of subpopulations) within a metapopulation viability model. We applied these tools to evaluate and inform an innovative management approach initiated by the Department of Defense (DoD), the Recovery Credit System for golden-cheeked warblers on Fort Hood.

Critical to determining the effects that various components within a stochastic metapopulation (SMP) model will have on overall viability are methods for determining the relationship between changes in model components and changes in metapopulation viability. Sensitivity analysis offers a direct avenue for quantifying these relationships by assessing how the output from a given model responds to changes in its inputs (Saltelli et al. 2000). Sensitivity analysis includes a wide range of methods that can be grouped into 2 general approaches: local sensitivity analysis and global sensitivity analysis (Saltelli et al. 1999). In local sensitivity analysis, model parameters are varied one at a time by a fixed amount while others are held to their original (i.e., best estimate) value. Local sensitivity to a parameter is measured by relating changes in the model output to the change in the parameter (sometimes normalized by the original value or standard deviation). Local sensitivity analysis has seen widespread use and because sensitivity values can usually be derived analytically through the use of partial derivatives, implementation is often straightforward. However, local measures of sensitivity can suffer when changes in parameters cause non-linear responses in the model output, when parameter uncertainty is not sufficiently characterized by a fixed change in the original value, when it is realistic to consider simultaneous changes in other model parameters, or when parameters interact. Many of these problems can be alleviated by employing a global approach to sensitivity analysis.

Global sensitivity analysis differs from local sensitivity analysis in two important ways. First, the full range of possible values for a parameter is explored to determine its effect on

model output. Second, the effect of the focal parameter on model output is averaged over possible variations of other model parameters. Because of the difficulty in relating model output to simultaneously varying and interacting inputs, several methods have been developed for global sensitivity analysis (Saltelli et al. 2000). However, most methods of global sensitivity analysis consist of the following steps:

1. The possible values for each of the j input parameters in a model are characterized by a probability (density) function D_j. Often these distributions are chosen to reflect the uncertainty in the parameter estimates but, depending on the goal of the sensitivity analysis, they may reflect natural variation or uncertainty related to the effects of management actions.

2. Repeated samples are selected from each distribution and these values are used as inputs for model evaluation. A unique model output is calculated for each of the replicate input samples.

3. The variation in model output caused by the varying inputs is related to the distribution D_j of each input parameter.

Some of the more prominent methods for global sensitivity analysis include regression-based approaches utilizing standardized partial regression coefficients and partial correlations as measures of sensitivity (Saltelli et al. 2000), the method of Sobol' (1993), and the extended Fourier amplitude sensitivity test (extended FAST; Saltelli et al. 1999). Sobol' indices and those derived from extended FAST are considered 'model independent' in that they do not rely on linear or near-linear relationships between the model outputs and the input parameters. Additionally, these methods allow the variance in the output attributable to variation in input parameters to be decomposed into first order effects as well as higher order effects caused by interactions among model parameters. Total effect indices are calculated by summing the first order effects with each additional higher order effect. Thus, they allow for the importance of interactions among model parameters to be quantified in relation to model output.

Using sensitivity analysis to inform conservation decisions based on population projection models has become increasingly popular and sophisticated. One of its earliest uses was in evaluating life-history characteristics of California condors that make the species particularly vulnerable to extinction (Mertz 1971). This study used manual perturbation, a form of local sensitivity analysis, to change vital rates and evaluated the effect these changes had on the likelihood of the population's persistence. Manual perturbation continues to be a popular method for conducting a sensitivity analysis on PVA models. However, several alternative approaches (see Mills and Lindberg 2002 for a review) have been developed including analytical sensitivity and elasticity analysis (Goodman 1971, Caswell 2001); life-table response experiments (Caswell 1989); and regression-based approaches (McCarthy et al. 1996, Wisdom and Mills 1997, Wisdom et al. 2000).

Methods

Generally, methods for conducting sensitivity analyses of PVA models have been developed for single population models. Although some of these methods could be applied to metapopulation viability models, upon initiation of our research it was unclear if and how researchers were performing sensitivity analyses on metapopulation viability models. Therefore, to determine the state of affairs in conducting a sensitivity analysis of SMP models, we surveyed the literature for studies in which a sensitivity analysis was conducted on metapopulation viability models. As part of this survey, we recorded the method used; whether the method was local or global; the stated purpose of the sensitivity analysis; the response variable; and which parameters were determined to be most sensitive. We also noted if there was publicly available software for conducting the sensitivity analysis.

Results of this survey showed that 87% (33 of 38 studies) of the sensitivity analyses on metapopulation viability models were considered "local" in that parameters were manually perturbed by a fixed amount around the nominal value. Additionally, for all but one of these 33 studies, parameters were changed one at a time with all other parameters held constant at their nominal value. The five studies that employed a "global" approach relied on linear models to relate changes in parameters to changes in metapopulation viability. None of the studies we examined used the more recent model independent methods of Sobol' and extended FAST. While these model independent methods are a relatively recent addition to the suite of methods for conducting a sensitivity analysis, they are beginning to see use in other areas of ecological research (e.g., Fieberg and Jenkins 2005). The paucity of studies using global sensitivity analysis on SMP models is likely due to the lack of software for conducting these analyses (Naujokaitis-Lewis et al. 2009). Most of the studies in our survey (26 of 38) used either RAMAS (Akçakaya 2005) or VORTEX (Lacy et al. 2007) to model metapopulation viability and neither of these popular programs contain the functionality for conducting a global sensitivity analysis. We note that during this project, a similar review was published by Naujokaitis-Lewis et al. (2009) which arrived at similar conclusions.

Because we consider the ability to conduct a global sensitivity analysis of SMP models paramount to meeting the objectives of our research, we developed new software (MetaPVA) to meet these needs. The usefulness of this software depended on two linked components (1) a demographically-based stochastic metapopulation model and (2) functionality for conducting several of the most popular methods of sensitivity analysis. The structure of the SMP model was guided by a review of well-established articles on topics such as single-population viability analysis (e.g., Leigh 1981, Dennis et al. 1991, Foley 1997), island-biogeography (e.g., MacArthur and Wilson 1967, Brown and Kodric-Brown 1977), source-sink dynamics (e.g., Pulliam 1988), fragmentation (e.g., Stacey and Taper 1992), and metapopulation ecology (e.g., Quinn and Hastings 1987, Harrison and Quinn 1989, Gilpin 1990). From this review, the following parameters were suspected to have an appreciable effect on metapopulation dynamics:

(1) number of populations within the metapopulation, (2) initial size (i.e., number of individuals) of each population, (3) within-population dynamics (i.e., stochasticity, survival, fecundity, carrying capacity and form of density dependence), (4) correlations of vital rates among populations, and (5) movement rates among populations. The SMP model portrayed in MetaPVA contains functionality to incorporate all of these processes (Table 4). The model is an age/stage-matrix based population projection model that incorporates the effects of species- and age-specific parameters such as mean vital rates (i.e., fecundity and survival), variation in vital rates, and density dependence as well as effects due to metapopulation dynamics (i.e., number of populations, dispersal among populations, and correlations in vital rates among populations.

Table 4. Available features in MetaPVA for modeling metapopulation viability.

Features	Population-specific	Age/Stage-specific
Life history characteristics		
Stage matrices		
mean survival	X	X
mean fecundity	X	X
Types of density dependence		
none	X	X
ceiling	X	X
Ricker	X	X
Beaverton-Holt	X	X
Allee effects	X	
trend in carrying capacity	X	X
Stochasticity		
Demographic		
fecundity (Poisson process)	NA	NA
survival (binomial process)	NA	NA
dispersal (binomial process)	NA	NA
Temporal		
survival rate (normal or lognormal)	X	X
fecundity (normal or lognormal)	X	X
carrying capacity (normal)	X	
dispersal (normal)	X	
Population parameters		
spatial location of populations	X	
initial abundance	X	X
extinction threshold	X	
correlations in vital rates	X	
dispersal rates	X	X

Incorporating functionality for sensitivity analyses in MetaPVA was challenging. Because of the complexity, both in the structure of the model and the number of possible parameters, we had to develop a flexible user-interface that allowed users to calculate sensitivity metrics for model-specific parameters (e.g., juvenile fecundity of a specific subpopulation) while at the same time allowing users to group related parameters (e.g., survival of all stages and all subpopulations) for a single sensitivity metric. We settled on an approach similar to that used in program MARK (White and Burnham 1999) where a parameter index matrix (PIM) is used. Model parameters with unique indices are treated as separate parameters while those with the same index are grouped and viewed as a single parameter in the subsequent sensitivity analysis (Figure 20). Sensitivity analyses are performed by linking MetaPVA with the 'Sensitivity' package (Pujol 2007) for program R (free statistical and graphical software). Sensitivity methods include a "direct" method that simply provides model outputs for randomly generated replicate inputs, Morris's (1991) one at a time (OAT) screening method, logistic regression (McCarthy et al. 1996), regression analysis utilizing standardized partial regression coefficients and partial correlation coefficients (Saltelli et al. 2000), and extended FAST (Saltelli et al. 1999) (Figure 21).

Figure 20. User-interface of MetaPVA used to specify unique mean fecundity parameters for subsequent sensitivity analysis. A similar interface is used for other model parameters.
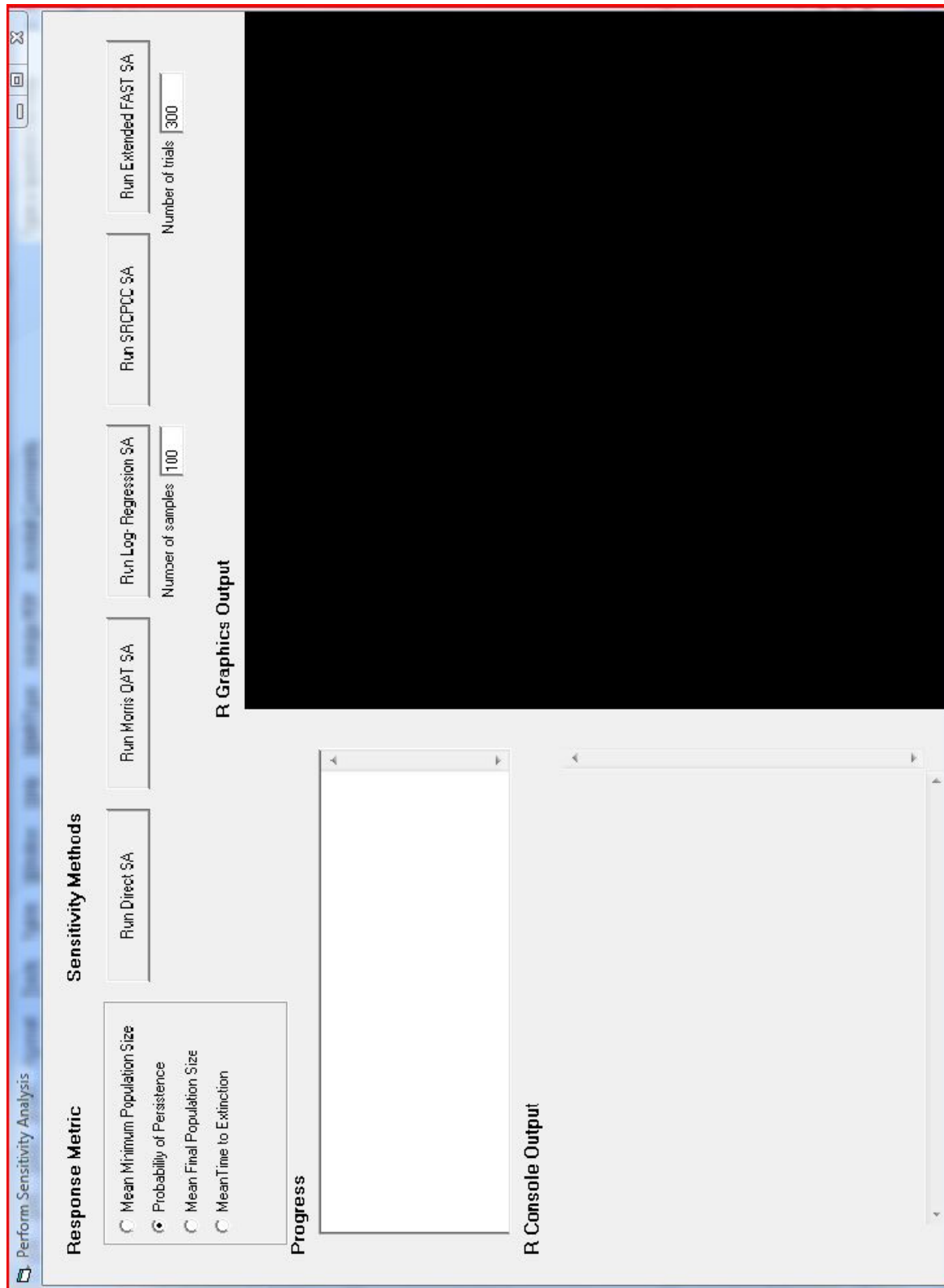
Figure 21. User-interface of MetaPVA for selecting the type of sensitivity analysis to perform on the metapopulation viability model.

MetaPVA completes each step required for conducting a sensitivity analysis of metapopulation viability models including a user-interface written in Visual Basic, calculation of sensitivity indices in R, and passing output from the sensitivity analysis back to the user-interface. The SMP model and options included in MetaPVA are similar to those contained in the proprietary software RAMAS Metapop (Akçakaya 2005). However, because MetaPVA was developed as a part of this project, a similar version will be made available to DoD for conducting metapopulation viability analyses. One key feature of this program is the ability to call and execute functions in R. This feature allows MetaPVA to utilize robust statistical procedures for generating random correlated deviates from a variety of distributions as well as the ability to include R packages (i.e. the sensitivity package).

Results and Discussion. Management of the Golden-cheeked Warbler Metapopulation, Fort Hood

Due to the challenges of managing species listed under the Endangered Species Act on private lands, much of the responsibility for conservation and recovery has traditionally been placed on public lands owned by the U. S. federal government and the various states. However, listed species rarely occur solely on public lands. Approximately two-thirds of listed species have populations on private lands (Groves et al. 2000), and as many as 37% depend entirely on non-federal lands for their habitat (GAO 1995). Moreover, populations of listed species that occur on individual tracts of public land usually represent only a fraction of a metapopulation, regional population, or species range. Thus, for the majority of these species, effective recovery strategies must involve management of both public and private lands (Wilcove and Lee 2004).

Despite the importance of private lands for the recovery and conservation of listed species, considerable conflict has arisen due to concerns about private property rights and the distribution of conservation costs (Bean and Wilcove 1997, Doremus 2003). Therefore, a growing number of programs seek to alleviate these conflicts by replacing regulatory measures with incentive-based mechanisms (Doremus 2003, Wilcove and Lee 2004). Such conservation incentive programs are designed to promote stewardship of endangered species habitat through voluntary conservation activities by landowners who are rewarded, financially or otherwise, for their participation (Bonnie 1999, Doremus 2003, Wilcove and Lee 2004). Conservation incentives range from Safe Harbor agreements (USFWS 1999) to landowner conservation assistance programs to market-based systems. Market-based incentive programs such as conservation banks can provide financial gain to landowners willing to conserve habitat and then sell "credits" to developers seeking mitigation (Wilcove and Lee 2004, Bean 2006). Recently, a market-based incentive program for the golden-cheeked warbler (*Dendroica chrysoparia*) has been implemented as a "proof of concept" in conjunction with habitat protection on Fort Hood, an 87,890 ha Army training post in central Texas (Figure 22).
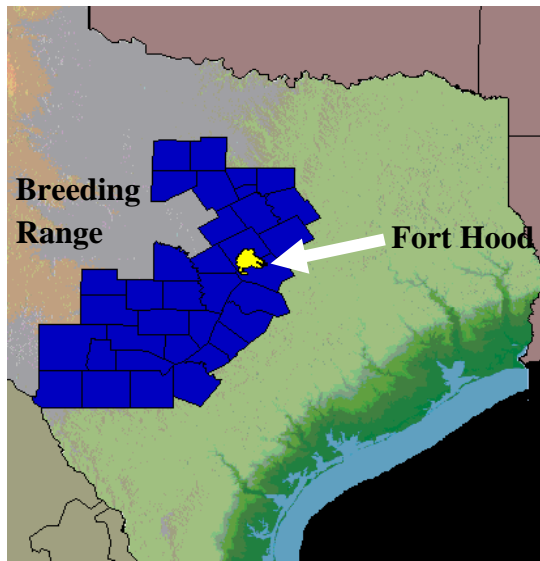
Figure 22. Location of Fort Hood in relation to golden-cheeked warbler breeding range (blue) in central Texas.

The golden-cheeked warbler is a neotropical migrant songbird that breeds in mature, closed-canopy woodlands composed primarily of Ashe juniper (*Juniperus ashei*) and oak (Quercus sp.) (Pulich 1976, Ladd and Gass 1999). Breeding range is confined to fewer than 36 counties in central Texas (USFWS 1996). Historically (pre-European settlement), breeding habitat was probably relegated to fragmented patches along streams and rocky limestone outcrops where oak-juniper woodlands could reach maturity (Kroll 1980). However, clearing of Ashe juniper for urban expansion, agriculture, and commercial harvest has further reduced and fragmented available breeding habitat resulting in the golden-cheeked warbler being listed as Endangered in 1990 (USFWS 1990). Protection of existing breeding habitat has been cited as an important component of golden-cheeked warbler recovery (USFWS 1992). Effective habitat management on both public and private lands is particularly important for the golden-cheeked warbler as most breeding habitat occurs on privately owned land (USFWS and Environmental Defense 2000).

Fort Hood contains the largest breeding population of golden-cheeked warblers under a single landowner (USFWS 1992). Recent population estimates on Fort Hood range from 2,901 to 6,040 territorial males (Cornelius et al. 2007) and Anders and Dearborne (2004) suggested a stable or slightly increasing population trend since 1992. However, despite optimistic population sizes and trends and the relative security of breeding habitat, a viable population of golden-cheeked warblers on Fort Hood is not guaranteed. In addition to the possibility of natural catastrophes and increased demands for military training, live munitions will always pose a fire

threat to breeding habitat. In fact, much of Fort Hood's active management is in response to a 1996 wildfire that destroyed or damaged ~2,100 ha, approximately 15% of the available breeding habitat at that time (Cornelius et al. 2007). As such, managers at Fort Hood must consider the possibility that unintentional loss of habitat on Fort Hood will jeopardize the overall viability of golden-cheeked warblers and lead to more stringent training restrictions in the future. To guard against this scenario, in 2006 the DoD began a 3-year trial of the Recovery Credit System (RCS), which provides Fort Hood with recovery credits for funding conservation of golden-cheeked warbler habitat on private lands (USFWS 2007). Under the RCS, recovery credits accumulated by Fort Hood through contracts with private landowners would be used to offset unanticipated loss of golden-cheeked warbler habitat within the boundaries of the installation.

Critical to successful implementation of market-based incentive programs such as the RCS is the ability to assign a value, in terms of changes to population viability, to both habitat loss and potential habitat restoration or protection. In particular, if a certain amount of habitat is lost in one area, how much habitat needs to be restored or protected in another area such that there is no change in overall viability? Applied ecologists have considered the relative conservation value of patches differing in size and connectedness since the development of island biogeography (MacArthur and Wilson 1967, Brown 1971) and metapopulation theory (Hanski and Gilpin 1991). But despite the recognition that habitat patches vary in their contribution to viability, the specifics of any one system may be hard to generalize, suggesting that the value of habitat losses and gains should be evaluated quantitatively based on species-specific models of metapopulation dynamics (Doak and Mills 1994, Bruggeman and Jones 2008). We describe an approach for applying sensitivity analysis to a metapopulation projection model to evaluate how changes in golden-cheeked warbler breeding habitat, both on and off Fort Hood, might affect overall species viability. Specifically, we sought to answer the following questions: Given the same amount of change in breeding habitat, does the change in some patches have a greater effect on overall persistence of the metapopulation than others? If so, can characteristics of a patch (e.g., size or its spatial location) be used to predict how the metapopulation will respond to these changes?

Analytical Approach

We assessed golden-cheeked warbler viability using a demographically-based metapopulation model in which distinct patches of habitat support local breeding populations. The model structure and parameters were based on a previous study by Alldredge et al. (2004) who assessed the viability of the golden-cheeked warbler metapopulation in central Texas. However, to more effectively evaluate the questions for our study, we generalized the number and size of populations as well as their spatial arrangement. Therefore, we modeled 10 hypothetical populations with sizes, measured as the number of territories supported, ranging from 238 to 12,371. These values correspond to the smallest and largest (i.e., Fort Hood) populations modeled by Alldredge et al. (2004). To investigate the relationship between the

spatial location of a population and its importance, we arrayed the populations spatially so as to have a mix of sizes and relative distances from Fort Hood (Table 5).

Table 5. Characteristics of 10 hypothetical patches used to investigate the relationship between patch importance and patch size or distance from largest patch.

Patch Id	Patch Size (K)[a]	Distance from largest patch[b]
Pop1	238	1
Pop2	250	7
Pop3	300	4
Pop4	350	2
Pop5	400	8
Pop6	550	5
Pop7	700	3
Pop8	1000	6
Pop9	6000	9
Pop10 (e.g, Fort Hood)	12371	0

[a] Patch size is based on a classification of golden-cheeked warbler habitat and corresponds to the number of territories a habitat patch can support at ~4.5 ha per territory (i.e., the carrying capacity).
[b] Distance units are generic and were chosen to have a mix of sizes and distances from the largest patch.

We used a stochastic, discrete-time projection model based on stage-specific estimates of mean survival (S) and fecundity (F) as well as various assumptions about dispersal among populations. We modeled 3 age classes (i.e., stages) including hatch year (HY), second year (SY), and after-second year (ASY). The model was made stochastic by including temporal variation in survival and fecundity where the value of these parameters was randomly drawn during each time step (F_t, S_t) from a log-normal distribution (Akçakaya 2005). We also modeled demographic stochasticity by drawing the actual number of young reproduced per individual from a Poisson distribution with mean equal to F_t and the actual number of survivors for each time step from a binomial distribution with probability equal to S_t and number of "trials" equal to the number of individuals (N_t). Because golden-cheeked warblers are territorial during the breeding season, we modeled density dependence by incorporating a "ceiling" carrying capacity (K). Thus, populations grew without any density dependence until the population exceeded K at which time the population was either truncated to K or the excess individuals became dispersers (see Model Scenarios section). Initial abundances for projecting future population sizes were set to 80% of K. We simulated 2000 replicate population trajectories for 20 years into the future and

used the mean (across replicates) final abundance (MFA) to assess golden-cheeked warbler viability.

Golden-cheeked warbler dispersal is poorly understood (Ladd and Gass 1999). Therefore, we included 5 model scenarios that reflected various assumptions of dispersal behavior. Because adults have strong site fidelity, for all scenarios including dispersal, only SY individuals (i.e., HY birds that survived and returned to breed the following year) were allowed to disperse (Ladd and Gass 1999, Alldredge et al. 2004). The first scenario, **NoD**, assumed no dispersal between populations. The second, **SymD**, assumed 15% symmetric dispersal among populations (Alldredge et al. 2004). For each time step, 15% of the population of SY individuals would disperse from each population with emigrants distributed equally among the remaining 9 populations. Thus, a particular population would receive $N_j*0.0167$ immigrants from each of the j populations. Because dispersal may have inherent survival costs, our 3rd scenario included a decrease in disperser survival related to distance traveled, **SurvD**. This scenario still assumed 15% dispersal at each time step but the proportion of individuals that survived to immigrate into other populations declined with distance from the source population. Because our distances were generic, we simply assumed a linear decline in survival from distance = 0 where survival rate was 1 to distance = 9 (i.e., furthest distance modeled) where survival rate was 0. Thus, a particular population would receive $N_j*0.0167*(1 - 0.111*D_j)$ immigrants from each of the j populations where D_j is the distance from the jth population. Our 4th scenario **KD** was based on the idea that SY individuals may be strongly philopatric and only disperse if the source population exceeds K. Therefore, the **KD** scenario assumed individuals in excess of K become dispersers and subsequently emigrate in equal proportion to all other populations in the metapopulation. The 5th scenario, **KSurvD**, was similar to **SurvD** in that dispersers from the **KD** scenario experienced a declining survival rate related to the distance from the source population.

There was little information on survival and fecundity for populations other than Fort Hood. Thus, for the previous 5 scenarios, we assumed survival and fecundity were the same for each population (Table 6). However, metapopulation dynamics can be highly sensitive to differences in vital rates among populations (Hokit and Branch 2003) and there are several reasons why it would be reasonable to assume golden-cheeked warbler reproduction and survival would vary with patch area (Robinson et al. 1995, Suorsa et al. 2004). To accommodate this possibility, we included a 6th scenario, **KSurvDVitals**, in which fecundity and HY survival for each population increased linearly with the size of the population (Table 7). The lower and upper limits of these values correspond to the minimum and maximum observed values reported in Alldredge et al. (2004).

Table 6. Golden-cheeked warbler mean survival (*S*) and fecundity *(F)* based on those reported in Alldredge et al. (2004). Minimum and maximum observed values are in parentheses.

Stage[a]	*S*	Temporal Variance (*S*)	*F*[b]	Temporal Variance (*F*)
HY	0.40 (0.30, 0.50)	0.058	0	0
SY	0.57 (0.57, 0.57)	0.010	1.2 (0.8,1.4)	0.024
ASY	0.57 (0.57, 0.57)	0.010	1.3 (1.1,1.7)	0.006

[a] Stages were hatch-year (HY) including birds age 0 to 1 year, second year (SY) including birds age 1 to 2 years and after second year (ASY) including birds >2 years old.
[b] Fecundity is the number of HY birds produced per individual SY or ASY bird.

Table 7. Golden-cheeked warbler mean survival (*S*) and fecundity (*F*) for each population under scenario **KSurvDVitals** as described in text.

Patch Id	Patch Size (K)[a]	S_{HY}	S_{AHY}	F_{HY}	F_{AHY}
Pop1	238	0.300	0.570	0.750	1.090
Pop2	250	0.300	0.570	0.751	1.091
Pop3	300	0.301	0.570	0.754	1.093
Pop4	350	0.302	0.570	0.756	1.095
Pop5	400	0.303	0.570	0.759	1.097
Pop6	550	0.305	0.570	0.768	1.104
Pop7	700	0.308	0.570	0.776	1.111
Pop8	1000	0.313	0.570	0.793	1.125
Pop9	6000	0.395	0.570	1.078	1.356
Pop10	12371	0.500	0.570	1.440	1.650

[a] Patch size is based on a classification of golden-cheeked warbler habitat and corresponds to the number of territories a habitat patch can support at ~4.5 ha per territory (i.e., the carrying capacity).

Conceptually, we wanted to determine whether changing the size of particular patches by the same amount resulted in a greater effect on overall viability than others. Thus, we determined how much the mean final abundance (MFA) of warblers changed in response to changes in a particular population's size (K), reflecting potential loss or gain of habitat. To quantify this relationship, we performed a sensitivity analysis (Saltelli et al. 2000) of the metapopulation projection model. We drew 500 sets of random carrying capacities K_j for each of the $j = 1$ to 10 populations from uniform distributions that ranged +/- 200 of the population's original K. Thus, each population regardless of its original size was varied by the same amount. For each of the 500 sets of carrying capacities, the metapopulation projection model was run and MFA was recorded. Changes in MFA were related to changes in each population's carrying capacity (K_j) via linear regression. We used regression coefficients to quantify a particular patch's leverage (L_j) on metapopulation viability, measured as the expected change in MFA due to changing the size of a particular patch (i.e., K_j) by one unit,

$$L_j = \frac{\Delta MFA}{\Delta K_j} \ .$$

We related 2 patch characteristics, original patch size (K_j) and distance (DL_j) from the largest patch (i.e., Fort Hood), to that patch's leverage (L_j). We used these characteristics because they are commonly used to value patches for conservation credits (USFWS 2007) and if quantifiable relationships exist, they could be used to inform future applications of RCS. Specifically, we modeled L_j, as a linear function of K_j and DL_j. Preliminary analyses suggested an exponential relationship between L_j and K_j so all models were fit using the natural logarithm of K_j. The global model was

$$L_j = \beta_0 + \beta_1 \ln\left[K_j\right] + \beta_2 DL_j + \beta_3 \ln\left[K_j\right] \times DL_j$$

All possible subsets where parameters β_1, β_2, or β_3 or equaled 0 were fit as competing models except for the aspatial scenarios (i.e., **NoD**, **SymD**, **KD**) for which we only allowed for the effect of K_j. To identify important characteristics for predicting patch leverage, we used Akaike's Information Criteria corrected for small sample bias (AICc) to rank competing models based on their predictive ability (Burnham and Anderson 2002).

Metapopulation projections and sensitivity analyses were performed using a program written in Visual Basic with calls to R (http://www.r-project.org/) for some statistical procedures.

Findings

  Overall metapopulation viability differed substantially among the 6 scenarios we modeled (Table 8). Notably, metapopulation viability was lower with 15% dispersal versus no dispersal whereas viability was higher when dispersal was density dependent (i.e., only individuals exceeding carrying capacity became dispersers). Metapopulation viability was greatest with density dependent dispersal and vital rates related to patch size (i.e., scenario **KSurvDVitals**).

Table 8. Golden-cheeked warbler metapopulation viability[a]. Total initial abundance for the metapopulation was 19943.

Scenario[b]	MFA
NoD	11182
SymD	9870
SurvD	7884
KD	13037
KSurvD	12212
KSurvDVitals	16879

[a] Viability was measured by mean final abundance (MFA).
[b] Scenarios reflect various assumptions of dispersal and patch-specific vital rates.

  Plots of MFA versus changes in each population's carrying capacity (K_j) suggested a linear relationship (Figure 23). Thus, regression coefficients (L_j) provided a reasonable measure of the expected change in MFA due to changing the size of a particular population. Among the 6 scenarios we modeled, there was no consistent relationship between the leverage of a particular patch and the characteristics of that patch. Instead, both the characteristic (i.e., patch size versus distance from the largest population) that best predicted patch leverage, as well as the magnitude of the relationship, changed under different model scenarios (Tables 9 and 10). With no dispersal (i.e., **NoD**), there was little evidence for a relationship between patch leverage and patch size or distance from the largest patch suggesting that changes in the size of a particular patch had the same effect on MFA regardless of the characteristics of the patch. For the 4 scenarios based on constant vital rates and dispersal among populations (i.e., **SymD**, **SurvD**, **KD**, and **KSurvD**), patch size was the best predictor of leverage and distance from the largest patch was a poor predictor (Figure 24, Table 9). For these scenarios, as original patch size increased, patch leverage decreased. This indicates that given the same amount of habitat loss or gain, changes to smaller patches have a greater effect on overall viability than larger patches. Conversely, when vital rates varied among populations (**KSurvDVitals**), distance from the largest patch was the best predictor of leverage and patch size was weakly related (Figure 25, Table 9). For this scenario, as distance from the largest patch increased, patch leverage decreased.
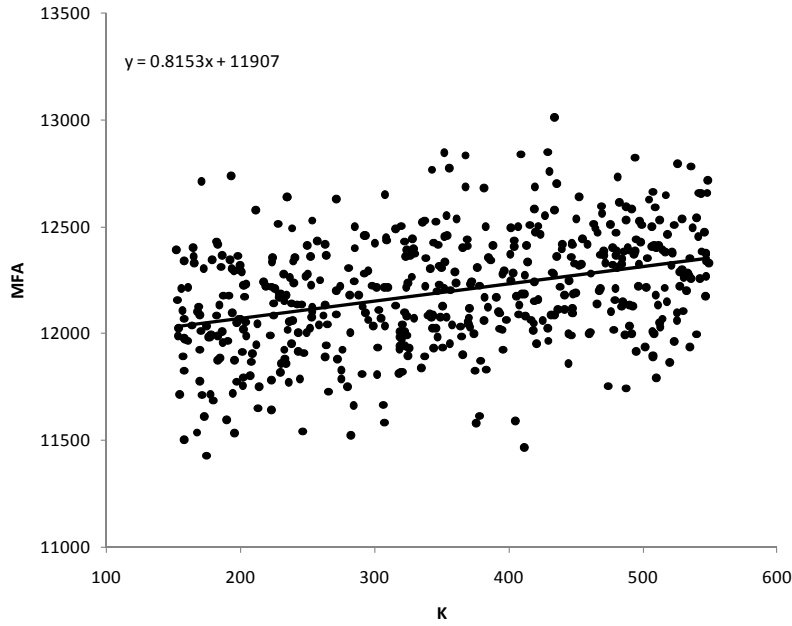
Figure 23. Example of the leverage metric ($L_4 = 0.81$) calculated for Population 4 under the KSurvD scenario. Leverage metrics were used to measure the expected change in mean final abundance (MFA) due to changing the size of a particular population (K).
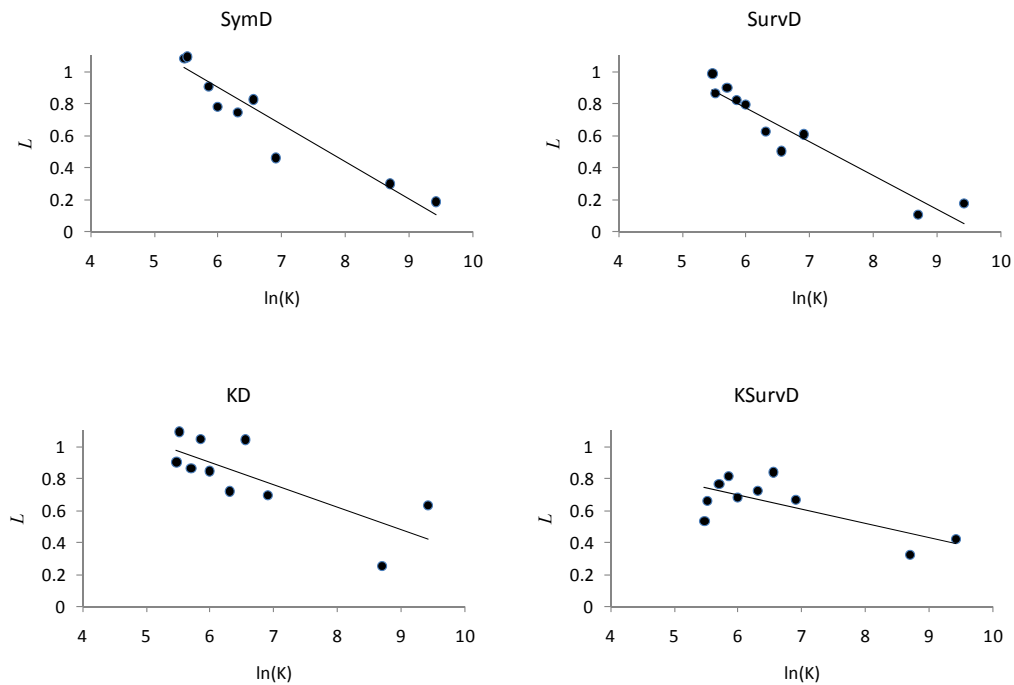
Figure 24. Relationships between patch leverage (L) and original patch size (K) for 4 dispersal scenarios (SymD, SurvD, KD, KSurvD) described in the text.

KSurvDVitals
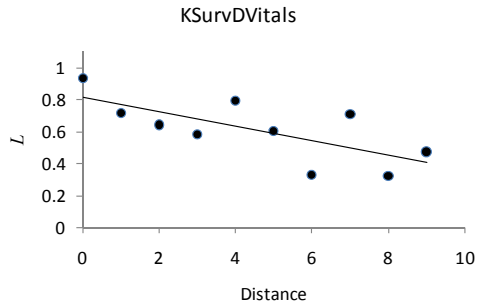
Figure 25. Relationships between patch leverage (*L*) and distance from the largest patch for the KSurvDVitals scenario described in the text.

Table 9. Model selection relating patch characteristics[a] to patch sensitivity.

Scenario[b]	Model	# Parameters	r^2	AICc	Delta AICc
NoD	null	2	NA	-16.4	0
NoD	ln(k)	3	0.08	-12.9	3.4
SymD	ln(k)	3	0.87	-5.1	0
SymD	null	2	NA	11.3	16.5
SurvD	ln(k)	3	0.91	-11.0	0
SurvD	null	2	NA	9.0	20.0
KD	ln(k)	3	0.59	0.8	0
KD	null	2	NA	5.4	4.5
KSurvD	ln(k)	3	0.52	-5.6	0
KSurvD	null	2	NA	-2.6	3.0
KSurvD	ln(k) + dist	4	0.54	-0.1	5.5
KSurvD	dist	3	0.02	1.5	7.1
KSurvD	ln(k) + dist + dist*ln(k)	5	0.58	8.1	13.6
KSurvDVitals	dist	3	0.50	-2.3	0
KSurvDVitals	null	2	NA	0.3	2.7
KSurvDVitals	ln(k) + dist	4	0.51	3.5	5.8
KSurvDVitals	ln(k)	3	0.02	4.5	6.8
KSurvDVitals	ln(k) + dist + dist*ln(k)	5	0.53	12.0	14.3

[a] Patch characteristics were the natural logarithm of patch carrying capacity (ln(k)) and distance from the largest patch (dist).
[b] Scenarios reflect various assumptions of dispersal and patch-specific vital rates as described in text.

Table 10. Parameter estimates (with standard errors in parentheses) of information theoretic (IT) best model(s)[a] relating patch leverage to patch characteristics[b].

Scenario[c]	IT Best Model	Intercept	ln(k)	dist
NoD	null	0.463 (0.027)	NA	NA
SymD	ln(k)	2.292 (0.210)	-0.232 (0.031)	NA
KD	ln(k)	1.745 (0.283)	-0.141 (0.042)	NA
SurvD	ln(k)	2.039 (0.157)	-0.211 (0.023)	NA
KSurvD	ln(k)	1.235 (0.206)	-0.089 (0.030)	NA
KSurvDVitals	dist	0.815 (0.086)	NA	-0.046 (0.016)

[a] Models presented are those with the lowest AICc score.
[b] Patch characteristics were the natural logarithm of carrying capacity (ln(k)) and distance from the largest patch (dist).
[c] Scenarios reflect various assumptions of dispersal and patch-specific vital rates as described in text.

Implications

      Conservation programs designed to offset unintentional loss of habitat on Fort Hood need to objectively value the importance of changes to off-post patches relative to changes in habitat on Fort Hood. This situation is not unique to Fort Hood. Indeed, many regulatory provisions require a means by which detrimental changes in ecological resources can be mitigated at the appropriate level by off-site compensation (Bruggeman and Jones 2008). We showed how sensitivity analysis of a stochastic population projection model could be used to quantify how changes in occupied habitat affect metapopulation viability. Thus, the importance of changes to individual habitat patches could be quantified in a rigorous and transparent analysis. For example, to determine how much habitat would need to be added or conserved in patch A to offset 50 lost territories in patch B, one would use the following

$$\Delta_A = \Delta_B \times \frac{\hat{L}_B}{\hat{L}_A}$$

If we assume dispersal scenario **KD**, that patch B initially held 250 territories and patch A held 6000 then,

$$\Delta_A = 50 \times \frac{1.74 - 0.14 \times \ln(250)}{1.74 - 0.14 \times \ln(6000)} = 93 \; .$$

So, enough habitat to accommodate approximately 93 territories would need to be added or conserved in patch A to offset the loss of 50 territories in patch B. This example emphasizes our counterintuitive result that under many of the most realistic scenarios (i.e., **SymD**, **SurvD**, **KD**, and **KSurvD**), *smaller* patches were expected to have higher leverage than larger patches where a unit change in *K* of these smaller patches leads to a larger change in mean final population size

in the future. This is important because in opposition to the dogma that "bigger is better," it suggests that given the *same* amount of habitat protection or restoration, it is better for future viability that these changes occur to smaller instead of larger patches.

By relating the characteristics of patches within the golden-cheeked warbler metapopulation to their importance, we investigated whether patch size or distance from the largest patch could be used to predict how influential changes to a particular patch would be to overall viability. However, we found it impossible to produce general guidelines for valuing habitat patches even within the limited set of scenarios we investigated. Without dispersal, changes to populations had an equivalent effect on overall viability. With dispersal, size of the patch was helpful in predicting patch leverage only when mean vital rates were the same among populations; otherwise distance from the largest patch was the best predictor. Based on our results, we suggest it would be dangerous to rely on general guidelines for valuing changes to habitat patches within a metapopulation. Instead, we recommend patches be valued based on changes to overall viability that are estimated via an explicit model of metapopulation dynamics.

Although our analysis did not produce consistent recommendations, it was useful in identifying critical model assumptions and parameters that should be targeted for future research. In particular, opposing conclusions of whether patch size or distance from the largest patch were important characteristics points to the need for better information on how habitat patches within the golden-cheeked warbler metapopulation are connected via dispersal and how mean survival and reproductive rates vary among patches. Additionally, we attempted to include several realistic assumptions about the golden-cheeked warbler metapopulation but, due to insufficient empirical data, recognize that our analyses did not cover all possibilities related to the spatial arrangement of habitat patches, patch-specific vital rates, spatial correlations in dynamics among populations, or effects of habitat fragmentation (i.e., edge effects; Murcia 1995). Despite these limitations, our analyses emphasize the fact that details matter and we stress the need to continue to refine and improve model parameters and assumptions to match the actual golden-cheeked warbler metapopulation. This can be accomplished by placing uncertainties in model structure, assumptions and parameter values within an adaptive management/research context (Bakker and Doak 2009). By doing so, model predictions can be evaluated with ongoing monitoring data and key components of the model (e.g., dispersal, patch-specific vital rates, etc.) can be targeted for future research (MacKenzie 2009).

PART 4: INCORPORATING MULTIPLE SOURCES OF UNCERTAINTY INTO POPULATION VIABILITY MODELS

Background

Population viability analysis (PVA) is "the application of data and models to estimate probabilities that a population will persist for specified times into the future" (Mills 2007:254) and is an important tool for assessing extinction risk and evaluating management options for species of conservation concern (Morris and Doak 2002). However, by their very nature (i.e., predicting the future), PVA models must accommodate some level of uncertainty. In fact, uncertainty in predictions (e.g., future population abundance) arise from 5 main sources: (1) the effects of future management actions, (2) choice of an appropriate simplified model structure to characterize complex ecological processes (i.e., model selection uncertainty), (3) unexplained or residual process variation in population dynamics not accounted for in the model, (4) uncertainty in the future values of environmental covariates (e.g., weather) that are included in the model, and (5) limited empirical data from which model parameters are estimated (i.e., estimation or sampling error). While this is not an exhaustive list (e.g., note the absence of demographic stochasticity and measurement error of empirical data), these major sources of variation translate to considerable differences in model predictions. For PVA to be informative, it is critical to be able to quantify the magnitude of uncertainty in model predictions and subsequently be able to assess whether the effects of management actions are significant enough to detect a change in viability despite this uncertainty. Concomitantly, if model components causing the uncertainty can be identified and prioritized, future research can target the components that are most likely to reduce overall prediction uncertainty.

Methods

We developed an approach, and accompanying computer code, to more completely quantify prediction uncertainty in PVA models. A similar framework was recently described by Bakker et al. (2009) for demographic-based models. Here we develop an approach for viability models based on time-series of abundance data (e.g., Dennis et al. 1991, Dennis and Otten 2000, Garton et al. 2011). The approach is based on uncertainty analysis (Saltelli et al. 2000) in which important components of prediction uncertainty are identified within a population viability model, empirical data are used to develop probabilistic distributions for uncertain inputs, and simulations are used to propagate these uncertainties and evaluate their influence on model predictions. We describe and demonstrate the approach with Sonoran pronghorn (*Antilocapra americana sonoriensis*), an endangered subspecies of North American pronghorn that is of great conservation and management concern in southern Arizona and to Barry M. Goldwater Range (BMGR). Our choice of Sonoran pronghorn was influenced by 4 motivations: (1) There is an urgent need to update a previous PVA done by Hosack et al. (2002), particularly related to evaluating the benefit of the captive breeding program; (2) the U. S. Fish and Wildlife Service (USFWS) has proposed to reestablish a new population within BMGR to aid in the recovery of wild Sonoran pronghorn; (3) there are now sufficient empirical data to fit population growth

models and quantify uncertainty in model inputs; and (4) the relatively complex dynamics among the captive population, current wild population and proposed reestablishment of a 2nd wild population allow for the construction of a general model/approach that can be transferred to other species of concern to the Department of Defense (DoD).

Results and Discussion: Quantifying Prediction Uncertainty in Population Viability Analysis of Sonoran Pronghorn at Barry M. Goldwater Range

Historically, Sonoran pronghorn were relatively common in wide alluvial valleys of the Sonoran Desert (USFWS 2009). Widespread decline began in the mid- to late-1800s due to competition with domestic livestock, fencing, and hunting which has reduced the current distribution to about 7.6 % of their original range (USFWS 2009). Sonoran pronghorn were federally listed as endangered in 1967 under the Endangered Species Preservation Act of 1966 and subsequently grandfathered in under the Endangered Species Act of 1973 (USFWS 1998). Most of the current U. S. population resides on the central portion of BMGR (BMGR-East) west of Arizona State Route 85 (SR 85) and adjoining Cabeza Prieta National Wildlife Refuge (CPNWR; Figure 26).
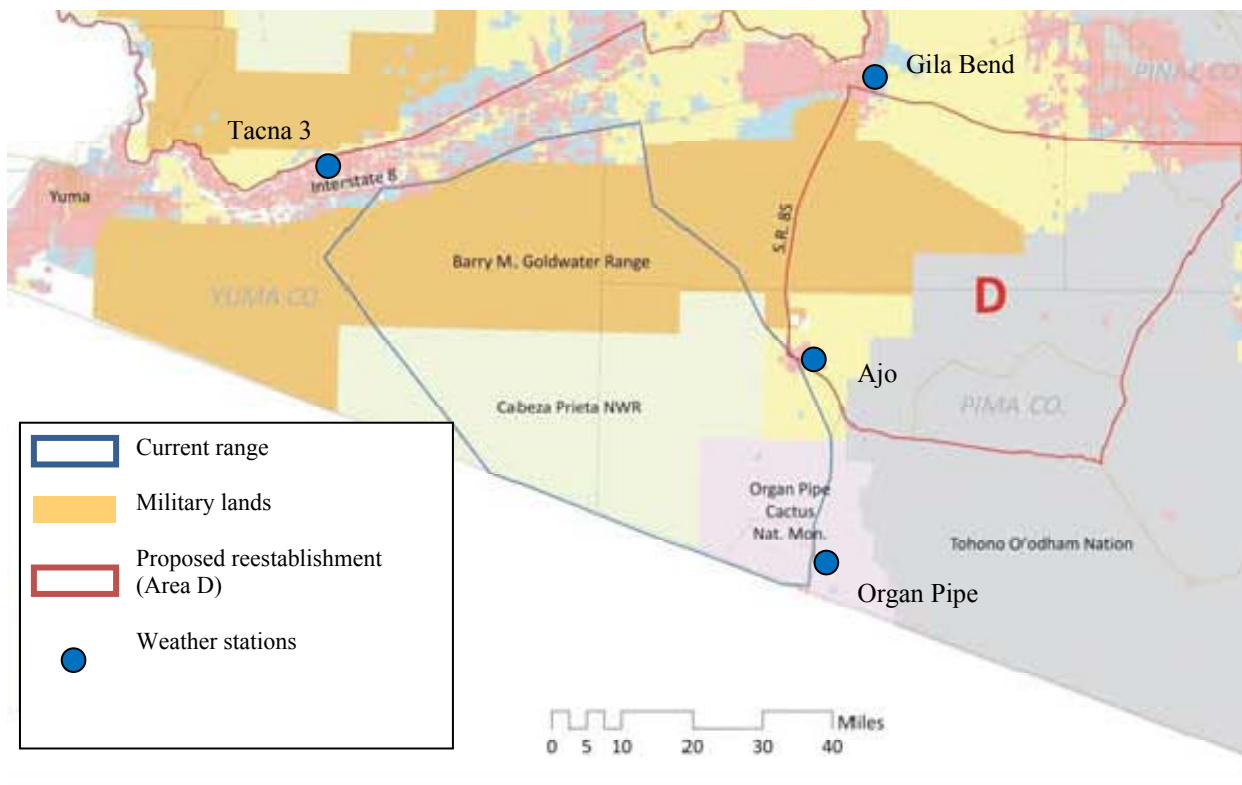
Figure 26. Location of current range of wild Sonoran pronghorn, Barry M. Goldwater Range, Cabeza Prieta National Wildlife Refuge, area of proposed reestablishment, and weather stations used for quantifying historic precipitation. Source: Draft Environmental Assessment for Reestablishment of Sonoran pronghorn, USFWS 2009.

In response to concern over the viability of Sonoran pronghorn, Hosack et al. (2002) conducted a PVA to determine extinction risks, identify model parameters whose estimation uncertainty had the greatest influence on estimates of viability, and evaluate changes in viability due to potential management actions. Viability was assessed using an individual-based, stochastic projection model (i.e., Vortex Version 7 software; Lacy et al. 1993) based on estimates of age at first reproduction for males and females, average fawn and adult survival, age-specific fecundity, temporal variation in survival and fecundity, impact of inbreeding depression, and maximum number of individuals the habitat can support (i.e., ceiling carrying capacity). In addition to these parameters, the model included effects of catastrophes and harvest on survival. The PVA of Hosack et al. (2002) was helpful in answering many of the outstanding questions that prompted their study. However, there are several reasons why a new PVA would be beneficial.

1. Estimates of key parameters and their temporal variation were acquired before the severe drought of 2002 which resulted in a historic low in the population size (i.e., and estimated 21 individuals).

2. In response to the small size of the wild population following this drought, a captive breeding pen was established at CPNWR which has subsequently been maintained and serves as a source for releases into the wild population.

3. The effect of supplementing the wild population from a captive population was assessed only in regard to inbreeding depression. The benefit of having a captive population to supplement the abundance of the wild population and buffer against stochastic lows in population size was not evaluated.

4. There are now sufficient empirical data (i.e., annual and bi-annual estimates of abundance) of both the wild and captive population to conduct a PVA based on alternative models of population growth (i.e., Dennis et al. 1991, Dennis and Otten 2000). This approach offers several advantages over a demographic-based PVA, including: (1) far fewer model parameters need to be estimated which can dramatically reduce the uncertainty in model predictions; (2) the ability to use previous abundance data to estimate the effects of density dependence and environmental drivers of population growth (e.g., precipitation) and incorporate these effects into the PVA; and (3) all parameters in the projection model, including their mean values, temporal variation, and estimation error are acquired from empirical data (i.e., time-series of past abundances and recorded precipitation).

5. In 2009, the USFWS proposed to establish additional populations within their historic range, including construction of an additional captive pen at Kofa National Wildlife Refuge (KNWR). The potential benefits of this proposal can be evaluated using population growth models mentioned above.

6. Improvements in techniques and the creation of computer programs with which to conduct an uncertainty/sensitivity analysis (Scott et al. 2010) allow for a more

comprehensive treatment of uncertainty in model predictions as well, as a way to identify future research needs to reduce uncertainty.

With these considerations in mind, we conducted a PVA of Sonoran pronghorn to meet the following objectives:

1. Make full use of past abundance data from both the wild and captive populations to model Sonoran pronghorn viability, including the potential effects of density dependence and key environmental drivers of population change (i.e., precipitation)
2. Quantify the change in viability of the current wild population due to immigration of individuals from the current captive population at CPNWR.
3. Quantify the change in the viability of the wild Sonoran pronghorn due to USFWS's proposed establishment of an additional wild population in BMGR-East.
4. Quantify the overall prediction uncertainty arising from parameter estimation error, environmental stochasticity, and uncertainties due to future management.
5. Identify the source(s) of prediction uncertainty that have the greatest influence and suggest how future research could reduce this uncertainty.

To achieve these objectives, we modeled 3 alternative management scenarios using stochastic models of population dynamics for the captive and wild population(s) of Sonoran pronghorn. The first management scenario was used to establish a baseline estimate of population viability without the potential benefits of the captive population at CPNWR or the reestablishment of an additional wild population. Thus for this scenario, we modeled the future viability of the current wild population with no immigrants from the captive population. The second scenario was used to evaluate the potential benefits of using the captive population at CPNWR to augment the current wild population. For this 2nd scenario, we modeled future viability of the current wild population with immigrants from the captive population at CPNWR. The 3rd scenario modeled future viability of wild Sonoran pronghorn by including the current wild population, the establishment of an additional wild population east of SR 85 on BMGR-East (Area D; Figure 26), and immigration into these populations from the captive population at CPNWR.

Analytical Approach

American pronghorn are polygynous (Byers and Moodie 1990) and thus, population dynamics are largely driven by changes in the females. Therefore, for all population growth models, we only considered the female population.

Because the captive population at CPNWR is mostly buffered from density dependent processes (i.e., overutilization of resources) and environmental conditions (e.g., precipitation), we modeled female abundance (*N*) by assuming a constant mean annual growth rate (μ) with annual variation in the realized growth rate caused by stochastic events experienced by the captive population (e.g., disease, predation, demographic stochasticity, etc.) Therefore, we modeled female abundance of the captive population at time *t* using

$$N(C)_{t+1} = N(C)_t \times \exp[\mu + Z_t \sigma_C] \qquad (1)$$

where $Z_t \sim normal(0,1)$.

Estimates of μ and σ_C were obtained from previous data of changes in female abundance where $\hat{\mu}$ was the average of the observed instantaneous growth rates ($r_t = \ln[N_{t+1}] - \ln[N_t]$) calculated each year and $\hat{\sigma}_C$ was the standard deviation of these growth rates (Table 11; Dennis et al. 1991).

Table 11. Changes in female abundance (N_t), adjusted to remove the effects of individuals introduced and removed individuals, within the captive population at CPNWR. Reconstructed from Sonoran Pronghorn Monthly Updates provided by Arizona Fish and Game and Arizona Antelope Foundation.

Year	Adults introduced	Reproduction	Fawn mortalities	Adult mortalities	Adults released	N_t	N_{t+1}	r_t
2004	6	0	0	0	0	6	8	0.287
2005	3	5	3	0	0	11	14	0.241
2006	3	4	0	1	0	17	24	0.344
2007	0	7	0	0	0	24	34	0.348
2008	0	11	1	0	0	34	41	0.187
2009	0	14	2	5	7	34		
							$\hat{\mu}$ =	0.282
							$\hat{\sigma}_C$ =	0.069

Precipitation is a major factor influencing wild Sonoran pronghorn survival (Bright and Hervert 2005). In addition, there is the possibility that negative density dependence (i.e., lower population growth rates at larger population sizes due to intraspecific competition) could also influence abundance. Therefore, we modeled the change in abundance of the wild population as a function of annual precipitation and previous abundance (e.g., Dennis and Otten 2000). Because abundance of the wild population is estimated every other year, the growth model depicted biennial changes in abundance.

$$N(W)_{t+2} = N(W)_t \times \exp\left[\beta_0 + \beta_1 \times N(W)_t + \beta_2 \times (\text{Precip}_t) + Z_t \sigma_W\right] \qquad (2)$$

where β_1 measures the magnitude of density dependence and β_2 measures the relationship between precipitation and the population growth rate and $Z_t \sigma_W$ represents residual or unexplained biennial variation in population growth. When β_1 and β_2 equal 0, the model reduces to that of exponential growth with mean annual growth rate equal to β_0. When β_2

equals 0, the model reduces to that of Ricker-type density dependence or Gompertz-type density dependence if previous abundance, $(N(W)_t)$, is log-transformed.

The variable for precipitation (Precip$_t$) quantifies the amount of precipitation that is believed to affect the change in population size during the interval t to $t + 2$. We measured Precip$_t$ by first averaging total monthly precipitation from 3 weather stations (i.e., Organ Pipe Cactus National Monument, station 026132; Ajo, station 020080; Tacna 3, station 028396; Western Regional Climate Center) within and proximate to the current range of wild Sonoran pronghorn (Figure 26). Next, we summed these monthly values across the two years between each abundance estimate. For example, if population abundance was estimated in December 1992 and again in December 1994, then Precip$_t$ was the sum of average monthly precipitation from January 1993 to December 1994.

We used biennial estimates of abundance from 1992 – 2008 (USFWS 2009) and corresponding measures of biennial precipitation (Table 12) to fit various forms of the growth model (equation 2) using multiple linear regression of the form

$$r_t = \ln\left[\frac{N(W)_{t+2}}{N(W)_t}\right] = \beta_0 + \beta_1 \times N(W)_t + \beta_2 \times (\text{Precip}_t) + Z_t\sigma_W .$$

(3)

Table 12. Changes in biennial precipitation (Precip$_t$) and abundance of wild Sonoran pronghorn from 1992 to 2008.

Year	Total abundance estimate	r_t	Precip$_t$
1992	179	0.455	18.75
1994	282	-0.774	6.59
1996	130	0.089	14.18
1998	142	-0.361	11.20
2000	99	-1.55	7.73
2002	21	1.02	15.80
2004	58	0.159	10.99
2006	68	0.000	13.17
2008	68		

We fit several models with and without the effects of density dependence and precipitation as well as models with log-transformed effects of abundance (i.e., Gompertz-type density dependence) and precipitation. The information-theoretic best model, as determined by Akaike's Information Criteria corrected for small sample size (AICc), was that growth of wild Sonoran pronghorn is dominated by the effect of precipitation (Table 13).

Table 13. Selection criteria and parameter estimates for population growth models fit to abundance estimates from 1992-2008 for the wild population of Sonoran pronghorn.

Model	AICc	AICc weight	r-squared	$\hat{\beta}_0$	$\hat{\beta}_1$	$\hat{\beta}_2$	$\hat{\sigma}_W$
$\beta_0 + \beta_2 * \ln(\text{Precip}_t)$	19.8	0.51	0.71	-4.72		1.87	0.39
$\beta_0 + \beta_2 * \text{Precip}_t$	20.5	0.37	0.69	-2.09		0.16	0.41
β_0	24.1	0.06	NA	-0.12			0.78
$\beta_0 + \beta_1 * \ln(N_t)$	27.1	0.01	0.28	-1.70	-0.52		0.62
$\beta_0 + \beta_1 * \ln(N_t) + \beta_2 * \text{Precip}_t$	27.4	0.01	0.77	-2.76	-0.30	0.14	0.35
$\beta_0 + \beta_1 * \ln(N_t) + \beta_2 * \ln(\text{Precip}_t)$	27.6	0.01	0.76	-4.93	-0.24	1.66	0.36
$\beta_0 + \beta_1 * N_t$	28.3	0.01	0.16	0.35	-7.77		0.67
$\beta_0 + \beta_1 * N_t + \beta_2 * \ln(\text{Precip}_t)$	29.1	0.00	0.71	-4.55	-0.93	1.82	0.39
$\beta_0 + \beta_1 * N_t + \beta_2 * \text{Precip}_t$	29.3	0.00	0.70	-1.81	-2.83	0.15	0.40

There was negligible difference in AICc and model fit (i.e., r-squared) between the model with log-transformed precipitation versus no transformation. For future projections we used the model with log-transformed precipitation because of slightly better selection criteria and fit and because it was more biologically plausible to assume population growth rate was most affected by precipitation at low amounts and became less affected as precipitation increased (Figure 27). Under this model, the 'equilibrium' (i.e., no population growth) precipitation level was 12.46 inches biennially. If biennial precipitation were above this amount, we would expect the population to increase. Conversely, if biennial precipitation were below this amount, we would expect the population to decrease.
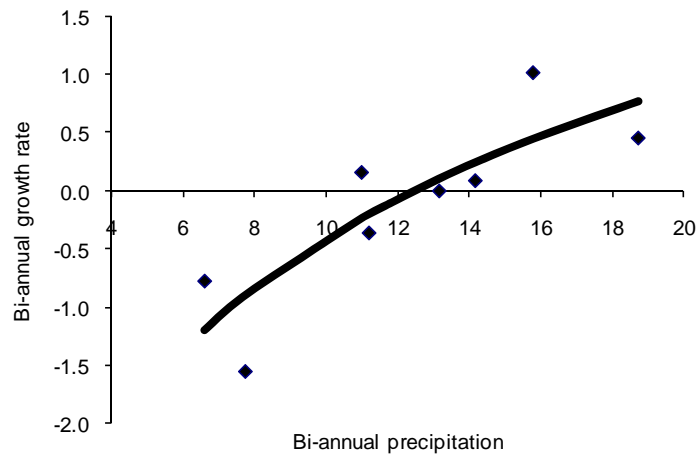
Figure 27. Relationship between biennial growth rate of the wild Sonoran pronghorn population and biennial precipitation. Fitted line depicts a linear relationship between growth rate and log-precipitation.

<u>Future population projection and viability</u>

The population viability model projected future abundance of Sonoran pronghorn based on the aforementioned growth models with parameter estimates obtained by fitting these models to previous abundance and precipitation data. Future abundance was projected for $t = 1$ to 20 time steps (years) and for stochastic models we simulated $j = 1$ to 4000 replicate trajectories. For all scenarios, initial abundances for the captive $N(C)_{j,0}$ and wild populations $N(W)_{j,0}$ were set to the last observed abundance for each (i.e., 34 females for the captive population and 34 females for the wild population, assuming a 50:50 sex ratio of males and females).

For the 1st scenario in which the current wild population receives no immigration from the captive population, we projected future abundance of the current wild population using

$$N(W)_{j,t+2} = N(W)_{j,t} \times \exp\left[\hat{\beta}_{0,j} + \hat{\beta}_{2,j} \times \ln\left(\text{Precip}_{j,t}\right) + Z_{j,t}\hat{\sigma}_{W,j}\right] \tag{4}$$

where $\hat{\beta}_0$, $\hat{\beta}_2$, and $\hat{\sigma}_W$ were the estimated values fit to past abundance and precipitation data and $Z_{j,t}$ was a random deviate from a standard normal distribution (i.e., mean = 0, std. deviation = 1).

For the 2nd scenario in which the current wild population continues to receive individuals from the CPNWR captive population, we projected future abundance using

$$N(W)_{j,t+2} = \left[N(W)_{j,t} + I(C)_{t+1} + I(C)_{t+2}\right] \times \exp\left[\hat{\beta}_{0,j} + \hat{\beta}_{2,j} \times \ln\left(\text{Precip}_{j,t}\right) + Z_{j,t}\hat{\sigma}_{W,j}\right] \tag{5}$$

where $I(C)_{t+1} + I(C)_{t+2}$ was the number of immigrants into the wild population from the CPNWR captive population. The number of immigrants to the wild population was determined by comparing the number of individuals in the captive population to a fixed capacity $K(C)$ for the enclosure, which we set at 34 adult females. If the number of individuals in the captive population exceeded the capacity of the enclosure, those excess individuals became emigrants available for transfer to the wild population. To determine the number of immigrants, we first projected future abundance of the captive population using

$$N(C)_{j,t+1} = N(C)_{j,t} \times \exp\left[\hat{\mu}_j + Z_{j,t}\hat{\sigma}_{C,j}\right] \tag{6}$$

At each time step, the size of the captive population was compared to the capacity of the enclosure, and the number of immigrants $I(C)_{t+1}$ into the wild population was calculated as

$$If \left[N(C)_{t+1} > K(C) \right] then$$

$$I(C)_{t+1} = N(C)_{t+1} - K(C)$$

and the abundance of the captive population reset to

$$N(C)_{t+1} = K(C).$$

Our 3rd scenario projected future abundance of wild Sonoran pronghorn in southern Arizona including the current wild population and the establishment of an additional wild population east of SR 85 on BMGR-East (Area D) with both wild populations receiving immigrants from CPNWR captive population. We projected future abundance of both the current wild population, now denoted with subscript 1 $N(W_1)$ to differentiate this population from the current wild population without the reestablished wild population $N(W_2)$, using

$$N(W_1)_{j,t+2} = \left[N(W_1)_{j,t} + Y_1 \times \left(I(C)_{t+1} + I(C)_{t+2} \right) \right] \times \exp\left[\hat{\beta}_{0,j} + \hat{\beta}_{2,j} \times \ln\left(Precip_{j,t} \right) + Z(W_1)_{j,t} \hat{\sigma}_{W,j} \right] \quad (7)$$

and

$$N(W_2)_{j,t+2} = \left[N(W_2)_{j,t} + Y_2 \times \left(I(C)_{t+1} + I(C)_{t+2} \right) \right] \times \exp\left[\hat{\beta}_{0,j} + \hat{\beta}_{2,j} \times \ln\left(Precip_{j,t} \right) + Z(W_2)_{j,t} \hat{\sigma}_{W,j} \right] \quad (8)$$

where $Z(W_1)_{j,t}$ and $Z(W_2)_{j,t}$ were standard normal deviates with a correlation of ρ and Y_1 and Y_2 were indicator functions governing whether emigrants from the captive population were sent to the current wild population or the reestablished population. We had no previous data to estimate ρ but assumed there would be some correlation in population growth rates (above and beyond the effect of precipitation) between the current and reestablished wild populations so we set $\rho = 0.5$.

The proposed protocol by USFWS governing movement decisions is described as follows (USFWS 2009:36):

> "…[When] there are additional Sonoran pronghorn available for release from the Cabeza Prieta NWR captive-breeding pen, moving and releasing these pronghorn into Area D would be considered for establishment of a third population. These relocation actions would occur when habitat conditions at Cabeza Prieta NWR are too poor to support additional wild pronghorn (i.e., those not in the breeding pen) or when the population of Sonoran pronghorn within the current U.S. range is greater than 140 animals."

Following these guidelines, immigrants from the captive population were moved to Area D, when the current U.S. population within the existing range was greater than 140 (i.e., 70 females

assuming a 50:50 sex ratio). Thus, if $\left[N\left(W_1\right)_t < 70 \right]$ then $Y_1 = 1$ and $Y_2 = 0$, otherwise $Y_1 = 0$ and $Y_2 = 1$. We did not include an option to make movements based on "poor" habitat conditions although it might be reasonable to make this choice dependent on localized precipitation. Because of an assumed barrier to movement imposed by SR 85, we did not allow any movements between the current and reestablished wild populations.

We placed 2 additional restrictions on all simulated population growth. First we set a limit on the realized finite growth rate $\left[N_{t+1} / N_t \right]$ equal to 2 based on the highest observed finite growth rate in the captive population (i.e.,. 1.86) and the highest reasonable biological limit (i.e., 3) which assumes 2 fawns per doe and 100% survival of does and fawns. The second restriction was a "ceiling" carrying capacity of both the current and reintroduced wild populations of 141 females (i.e., the highest observed abundance of the current wild population from 1992 – 2008 assuming a 50:50 sex ratio).

Prediction uncertainty

We ran future projections containing 4 levels of prediction uncertainty for each of the 3 management scenarios (i.e., no movement, movement only to the current wild population, and movement to the current and reestablished wild populations). The first level did not incorporate any uncertainty and was a deterministic projection of the wild populations. The second set of projections incorporated uncertainty due to parameter estimation error, future precipitation, and residual variation in growth models, each individually without the effect of the other two. The third contained all combinations for 2 of the 3 sources of prediction uncertainty (i.e., parameter estimation error and future precipitation, parameter estimation error and residual variation, future precipitation and residual variation). The 4th level contained all sources of uncertainty.

For simulations incorporating uncertainty due to residual or unexplained error (i.e., stochasticity) in population growth, simulations were run with the maximum likelihood estimates of σ_C and σ_W, otherwise these parameters equaled zero (i.e., projections were deterministic, except for possible uncertainty due to parameter estimation or future precipitation).

For simulations incorporating uncertainty due to parameter estimation error, we drew new estimates of model parameters for each replicate j from their respective sampling distributions. Thus, for the captive population, $\hat{\mu}_j$ was drawn from a normal distribution with mean = $\hat{\mu}$ and standard deviation = $SE\left(\hat{\mu}\right)$, the standard error, and

$$\hat{\sigma}_{C,j}^2 = V_j \frac{\hat{\sigma}_C^2}{q-1}$$

where q = number of observed rates of change (i.e., 5 for our captive population) and V_j was drawn from a chi-square distribution with $q - 1$ degrees of freedom (Dennis et al. 1991). For the wild populations, we used a parametric bootstrap with past abundance and precipitation data to

obtain new estimates of $\hat{\beta}_0$, $\hat{\beta}_2$, and $\hat{\sigma}_W$ for each replication. Thus, for each replicate j we simulated a new time series of past abundance data using

$$N(W)_{t+2} = N(W)_t \times \exp\left[\hat{\beta}_0 + \hat{\beta}_2 \times \ln\left(\text{Precip}_t\right) + Z_{j,t}\hat{\sigma}_W\right] \tag{9}$$

with an initial abundance set to half (assuming a 50:50 sex ratio of males and females) of the first estimated abundance in 1992, $N(W)_{j,0} = 89.5$, and precipitation values equal to those observed from 1992 - 2008. We then refit the model (equation 3) using this new time series of abundance to obtain $\hat{\beta}_{0,j}$, $\hat{\beta}_{2,j}$, and $\hat{\sigma}_{W,j}$.

For simulations incorporating uncertainty due to future precipitation, there were several alternatives. Analogous to our approach of using past abundance data to project future population dynamics, we based our projections of future precipitation on observed levels in the past. The 3 stations most proximate to the future distribution of Sonoran pronghorn are those we used to fit our population growth models (i.e., Organ Pipe Cactus National Monument, Ajo, and Tacna 3). However these stations only have reliable precipitation estimates back to 1969. Biennial precipitation from these stations during 1969 – 2008 suggested a declining trend (Figure 28a). However, a more complete record of past precipitation, 1899 – 2008, was available from the nearby Gila Bend weather station (Figure 26). For this extended time period, a similar declining trend in precipitation was not evident (Figure 28b). Therefore, as a conservative approach, we modeled future precipitation based on the 3-station average (i.e., Organ Pipe Cactus National Monument, Ajo, and Tacna 3) from 1993 – 2008 which coincided with the period during which wild abundance was modeled (see description of Precip variable described above). Based on these data, we did not include a trend in precipitation but instead drew a value of $\text{Precip}_{j,t}$ using the mean = 12.30 and standard deviation = 4.05 of biennial precipitation during this time.
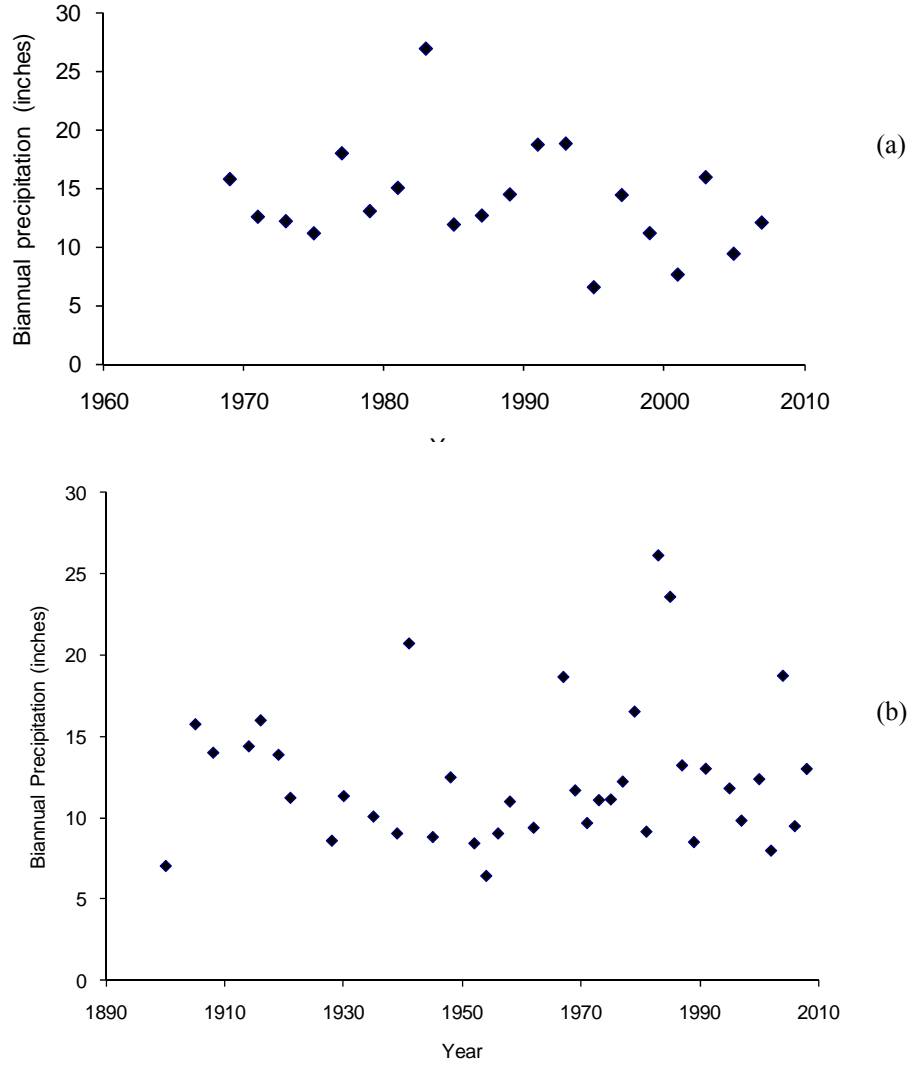
Figure 28. Historic biennial precipitation from 3-station (Organ Pipe Cactus National Monument, Ajo, and Tacna 3) average (a) and Gila Bend (b) weather stations. See Figure 26 for geographic locations of these stations.

We described prediction uncertainty by calculating a probability density surface for final abundances using a kernel density estimate implemented using the function "plot(density)" in R. We evaluated the contribution of each source of uncertainty by calculating the proportional reduction in total prediction uncertainty due to removing each source,

$$PR_s = \frac{[Var(total) - Var(\neq s)]}{Var(total)}$$

where Var(total) is the variance in final abundance with all sources of uncertainty and $Var(\neq s)$ is the variance in final abundance not including source (s). Model fitting and viability simulations were conducted using the statistical computing software R (www.r-project.org/).

Findings
Population Viability (no prediction uncertainty)

Mean biennial precipitation used in our simulations (i.e., 12.30 inches) was slightly below the precipitation level of 12.46 for which we would expect zero population growth. Therefore, the wild population would be expected to undergo a slight decline in abundance if future precipitation was held at the mean precipitation over the last 15 years and there was no immigration from the captive population. Thus, starting with 34 individuals, the final population size of current wild with population was 26 (Figure 29).

The expected number of immigrants $\bar{I}(C)$ from the captive population to the wild population(s) can be calculated by setting $N(C)_{t+1} = N(C)_t = K(C)$ so that the captive population is maintained at capacity by the removal of emigrants. Thus, the population growth model for the captive population, $N(C)_{t+1} = N(C)_t \times \exp(\mu) - I(C)_t$, would equal $K(C) = K(C) \times \exp(\mu) - \bar{I}(C)$. Solving for the expected number of immigrants to maintain this relationship, $\bar{I}(C) = K(C) \times [\exp(\mu) - 1]$. Finally, using the last number of females in the enclosure as the target capacity, $K(C) = 34$, and $\hat{\mu} = 0.2818$ estimated from previous data, the expected number of annual immigrants from that captive population at CPNWR is

$$\bar{I}(C) = K(C) \times 0.3255 = 11.06 . \tag{10}$$

Equation 10 indicates that the capacity of the captive population would have to be increased by approximately 3 individuals to increase the expected number of immigrants by 1.

Incorporating movements from the captive population to the current wild population, the final population size of the wild population without the reestablishment of an additional population was 141 (i.e., the limit imposed by the "ceiling" carrying capacity) and with reestablishment of an additional population was 220 (Figure 29).
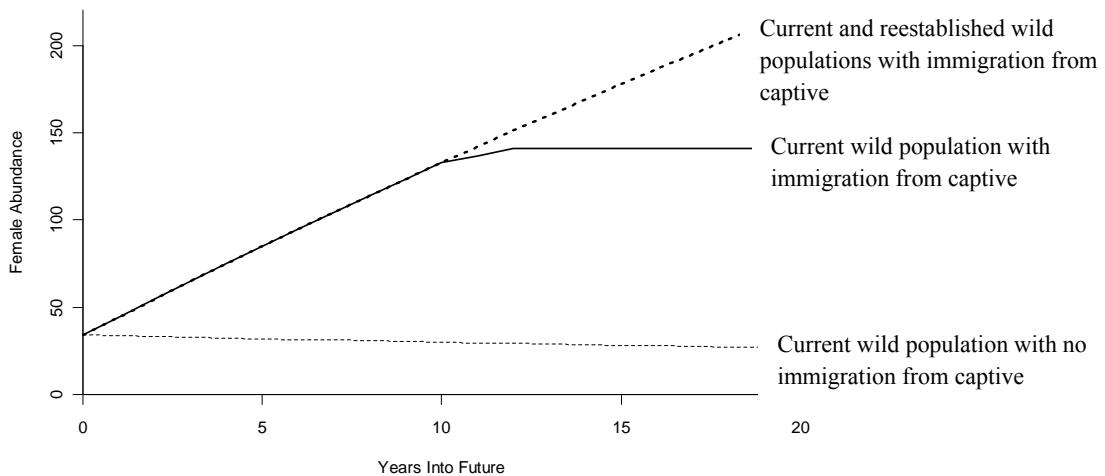
Figure 29. Deterministic projections of the wild Sonoran pronghorn 20 years into the future.

Population viability (residual uncertainty)

Including uncertainty due to unexplained (i.e., residual) variation in population growth resulted in probabilistic distributions for final population size (Figure 30). With this type of prediction uncertainty, the probability that the final wild population would be below 50 individuals was 0.73 without immigration from the captive population; 0.02 with immigration into the current wild population ; and 0.01 with immigration and the reestablishment of an additional population. The probability that the final wild poplation would be above 100 individuals without immigration from the captive population was 0.10; 0.74 with immigration into the current wild population; and 0.90 with immigration and the reestablishment of an additional wild population.
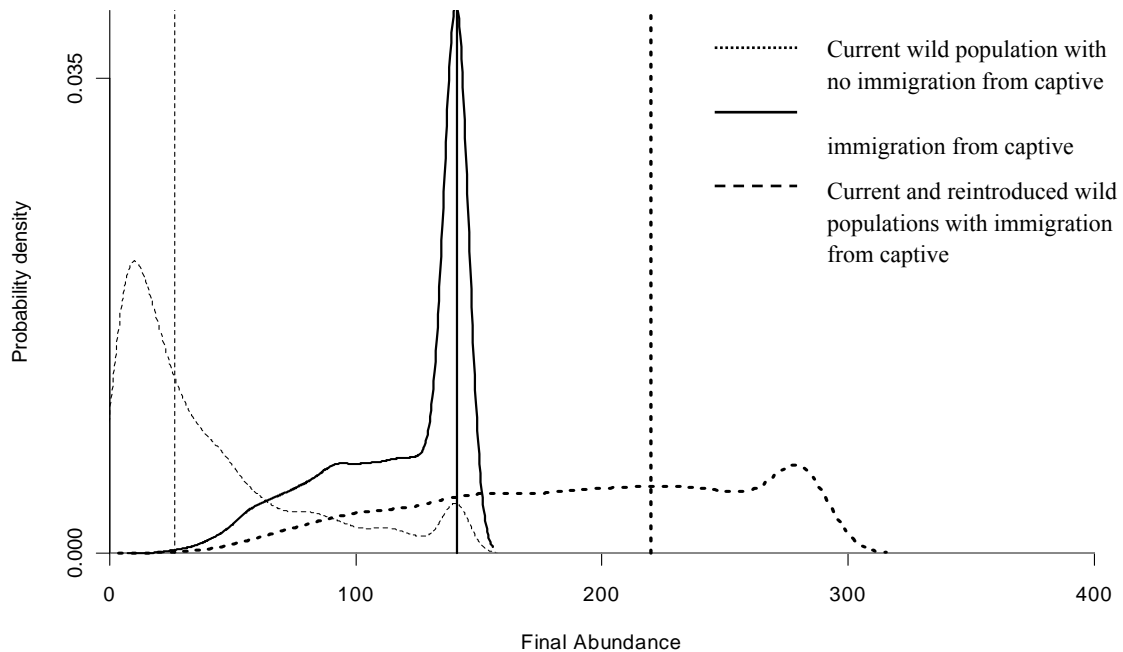
Figure 30. Probability density of final abundance of wild Sonoran pronghorn 20 years into the future based on population growth models that include unexplained or residual variation only. Vertical lines are final abundances from deterministic projections. Right-side peaks in the distributions are due to the "ceiling" carrying capacities (i.e., 141 individuals) imposed on these populations, thus final abundances were truncated at these values.

Population viability (parameter estimation uncertainty)

Including uncertainty due to parameter estimation error produced results similar to those
from including uncertainty due to residual variation in population growth models (Figure 31).
With this type of prediction uncertainty, the probability that the final wild population would be
below 50 individuals without immigration from the captive population was 0.65; 0.05 with
immigration into the current wild population; and 0.04 with immigration and the reestablishment
of an additional population.   The probability that the final wild poplation would be above 100
individuals without immigration from the captive population was 0.19; with immigration into the
current wild population was 0.74; and with immigration and the reestablishment of an additional
wild population was 0.83.
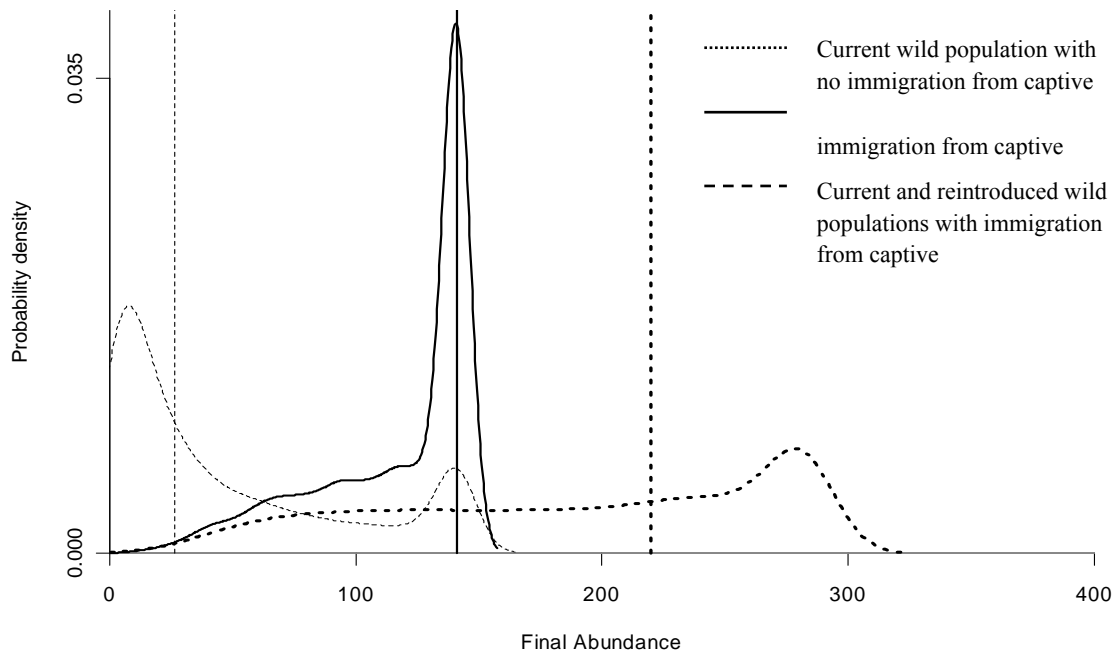
Figure 31. Probability density of final abundance of wild Sonoran pronghorn 20 years into the
future based on population growth models that include parameter estimation error only. Vertical
lines are final abundances from deterministic projections. Right-side peaks in the distributions
are due to the "ceiling" carrying capacities (i.e., 141 individuals) imposed on these populations,
thus final abundances were truncated at these values.

Population viability (uncertainty in future precipitation)

Including uncertainty due to future precipitation resulted in a greater likelihood of lower final population abundances than predictions including only residual variation or parameter estimation error (Figure 32). With this type of prediction uncertainty, the probability that the final wild population would be below 50 individuals without immigration from the captive population was 0.83; with immigration into the current wild population was 0.22; and with immigration and the reestablishment of an additional population was 0.18.   The probability that the final wild poplation would be above 100 individuals without immigration from the captive population was 0.08; with immigration into the current wild population was 0.51; and with immigration and the reestablishment of an additional wild population was 0.60.
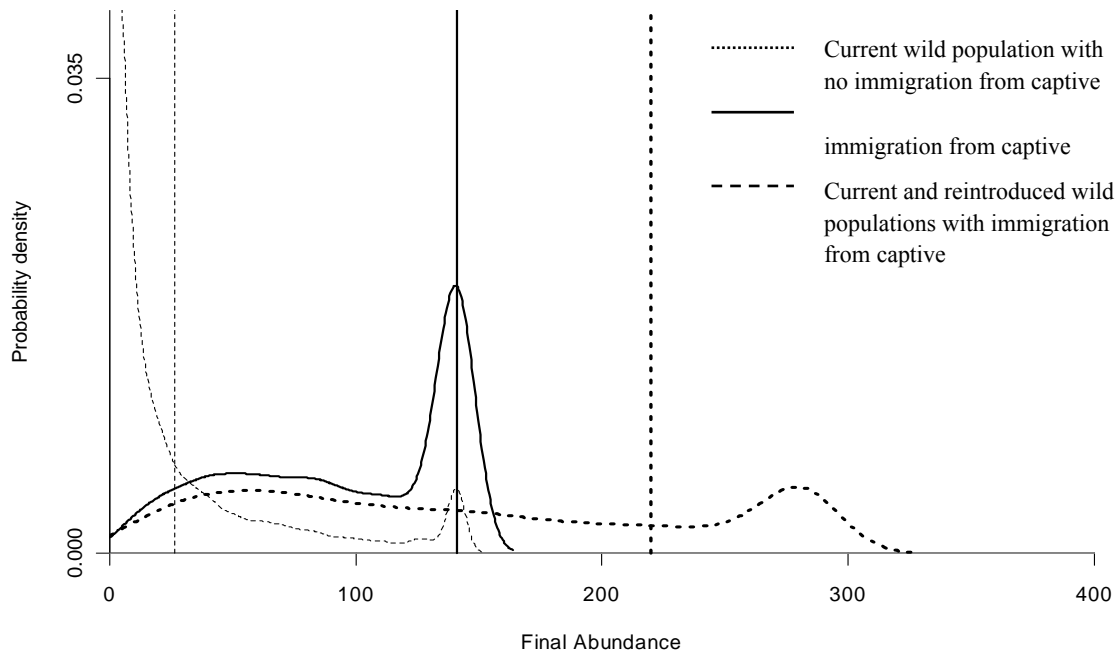
Figure 32. Probability density of final abundance of wild Sonoran pronghorn 20 years into the future based on population growth models that include parameter estimation error only. Vertical lines are final abundances from deterministic projections. Right-side peaks in the distributions are due to the "ceiling" carrying capacities (i.e., 141 individuals) imposed on these populations, thus final abundances were truncated at these values. Left-side peak in the distribution of the current wild population with no immigration from the captive population is not shown to retain a reasonable range on the y-axis.

Population viability (uncertainty from residual variation and parameter estimation)

     Prediction uncertainty due to residual variation in the population growth models and parameter estimation error was similar to that when these types were included individually (Figure 33). With these types of prediction uncertainty, the probability that the final wild population would be below 50 individuals without immigration from the captive population was 0.65; with immigration into the current wild population was 0.05; and with immigration and the reestablishment of an additional population was 0.03.   The probability that the final wild poplation would be above 100 individuals without immigration from the captive population was 0.20; with immigration into the current wild population was 0.73; and with immigration and the reestablishment of an additional wild population was 0.82.
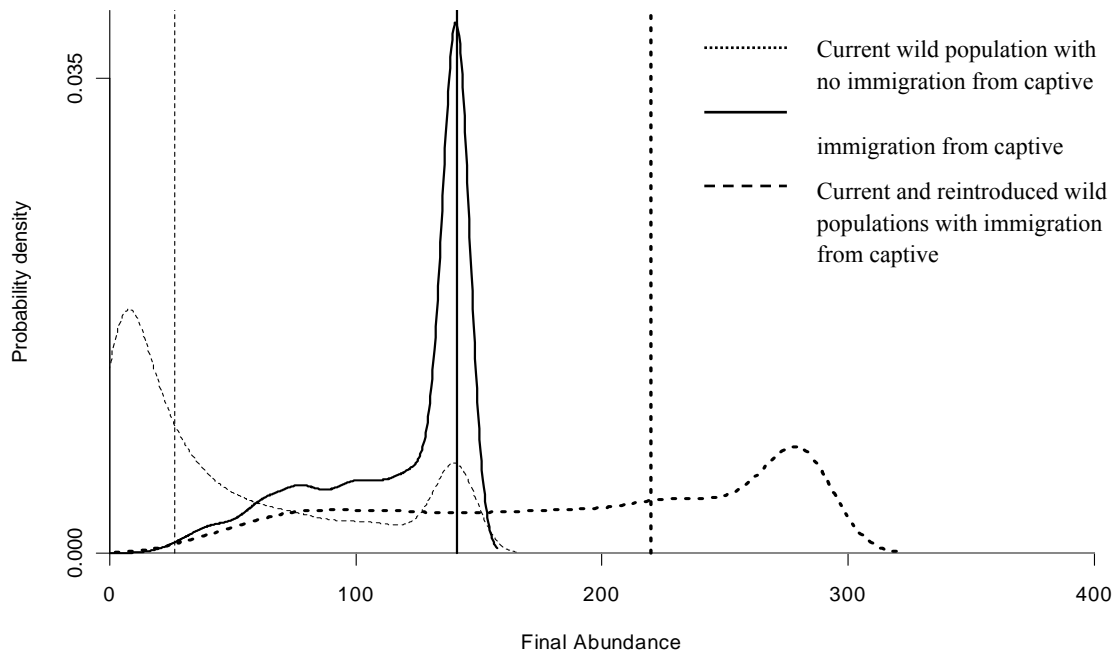
Figure 33. Probability density of final abundance of wild Sonoran pronghorn 20 years into the future based on population growth models that include residual variation and parameter estimation error. Vertical lines are final abundances from deterministic projections. Right-side peaks in the distributions are due to the "ceiling" carrying capacities (i.e., 141 individuals) imposed on these populations, thus final abundances were truncated at these values.

<u>Population viability (uncertainty from residual variation and future precipitation)</u>

Prediction uncertainty due to residual variation in the population growth models and future precipitation was similar to that when only precipitation was included (Figure 34). With these types of prediction uncertainty, the probability that the final wild population would be below 50 individuals without immigration from the captive population was 0.85; with immigration into the current wild population was 0.23; and with immigration and the reestablishment of an additional population was 0.20. The probability that the final wild poplation would be above 100 individuals without immigration from the captive population was 0.07; with immigration into the current wild population was 0.48; and with immigration and the reestablishment of an additional wild population was 0.59.
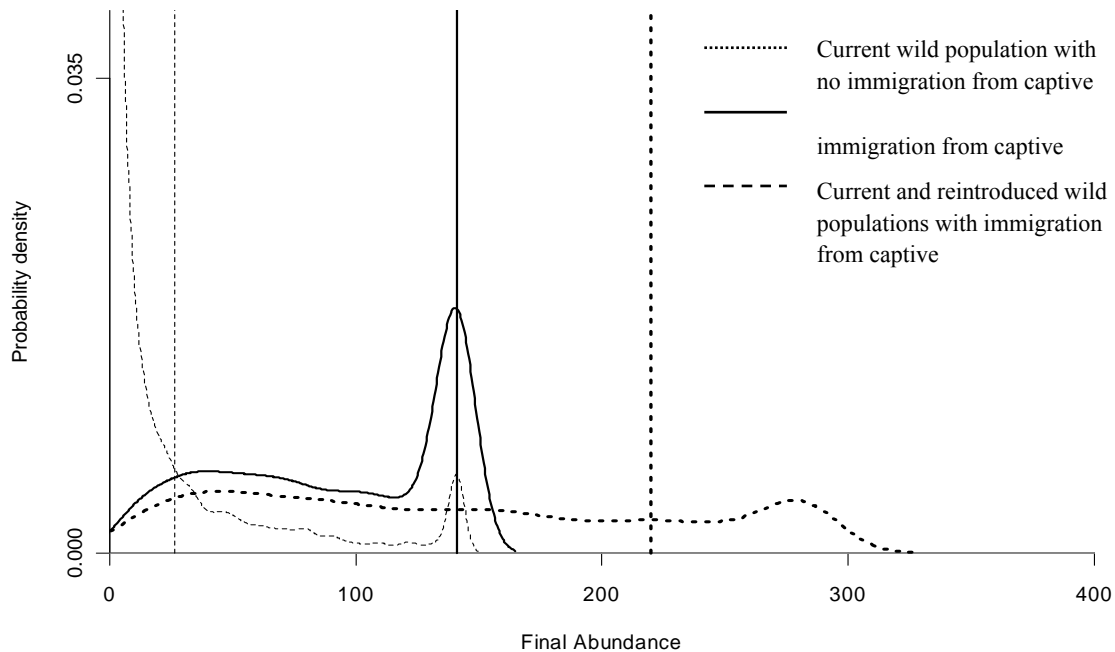
Figure 34. Probability density of final abundance of wild Sonoran pronghorn 20 years into the future based on population growth models that include residual variation and uncertainty in future precipitation. Vertical lines are final abundances from deterministic projections. Right-side peaks in the distributions are due to the "ceiling" carrying capacities (i.e., 141 individuals) imposed on these populations, thus final abundances were truncated at these values. Left-side peak in the distribution of the current wild population with no immigration from the captive population is not shown to retain a reasonable range on the y-axis.

<u>Population viability (uncertainty from parameter estimation and future precipitation)</u>

Prediction uncertainty due to parameter estimation error and future precipitation was similar to that when only precipitation was included (Figure 35). With these types of prediction uncertainty, the probability that the final wild population would be below 50 individuals without immigration from the captive population was 0.83; with immigration into the current wild population was 0.25; and with immigration and the reestablishment of an additional population was 0.21. The probability that the final wild poplation would be above 100 individuals without immigration from the captive population was 0.09; with immigration into the current wild population was 0.48; and with immigration and the reestablishment of an additional wild population was 0.58.
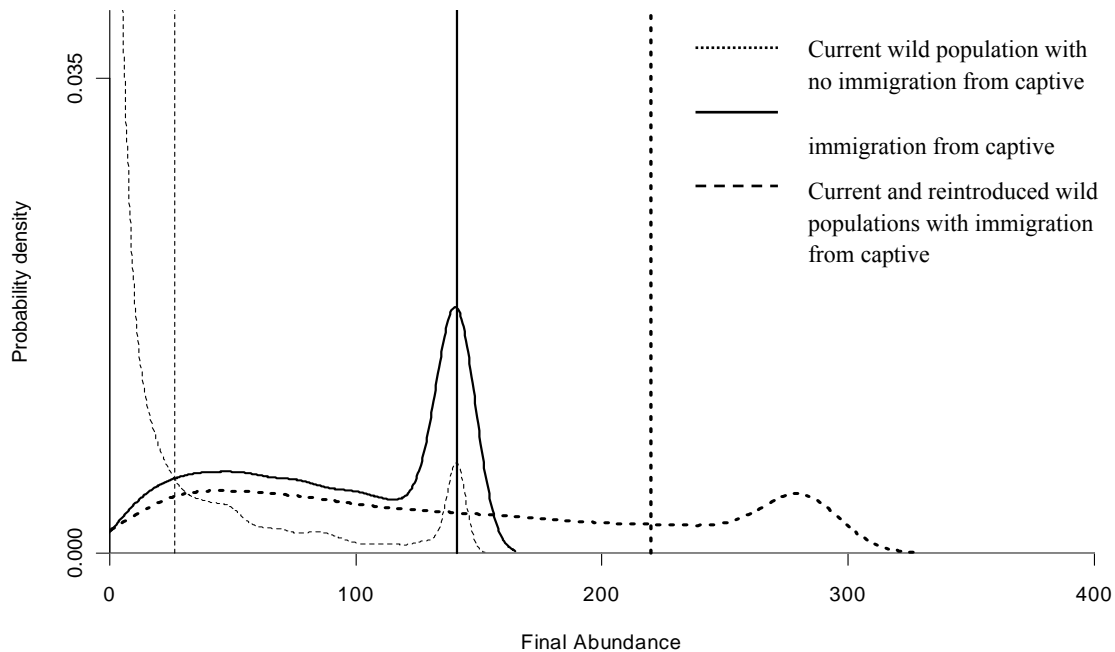
Figure 35. Probability density of final abundance of wild Sonoran pronghorn 20 years into the future based on population growth models that include parameter estimation error and uncertainty in future precipitation. Vertical lines are final abundances from deterministic projections. Right-side peaks in the distributions are due to the "ceiling" carrying capacities (i.e., 141 individuals) imposed on these populations, thus final abundances were truncated at these values. Left-side peak in the distribution of the current wild population with no immigration from the captive population is not shown to retain a reasonable range on the y-axis.

<u>Population viability (all sources of uncertainty)</u>

Prediction uncertainty when all sources (i.e., residual variation, parameter estimation, and future precipitation) were included was similar to previously described subsets that included uncertainty in future precipitation (Figure 36). With these types of prediction uncertainty, the probability that the final wild population would be below 50 individuals without immigration from the captive population was 0.82; with immigration into the current wild population was 0.26; and with immigration and the reestablishment of an additional population was 0.21. The probability that the final wild poplation would be above 100 individuals without immigration from the captive population was 0.09; with immigration into the current wild population was 0.48; and with immigration and the reestablishment of an additional wild population was 0.57.
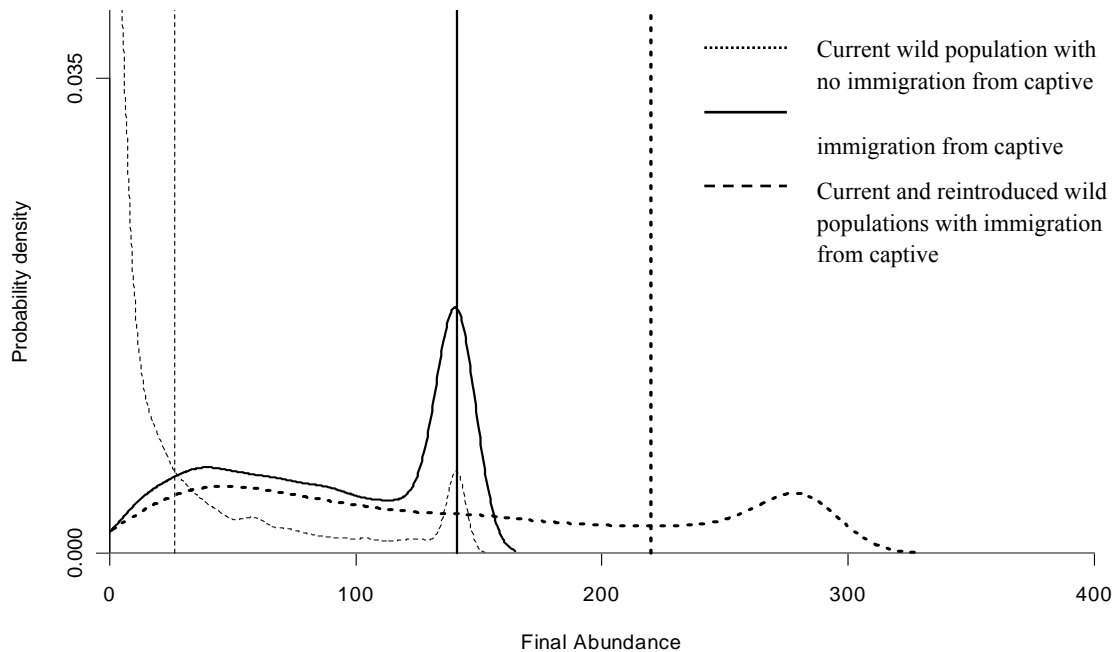
Figure 36. Probability density of final abundance of wild Sonoran pronghorn 20 years into the future based on population growth models that include all sources of prediction uncertainty (i.e., residual variation, parameter estimation error, and uncertainty in future precipitation). Vertical lines are final abundances from deterministic projections. Right-side peaks in the distributions are due to the "ceiling" carrying capacities (i.e., 141 individuals) imposed on these populations, thus final abundances were truncated at these values. Left-side peak in the distribution of the current wild population with no immigration from the captive population is not shown to retain a reasonable range on the y-axis.

Component contributions to overall uncertainty

For the management scenario including the reestablishment of an additional wild population and including immigration from the CPNWR captive population, uncertainty in future precipitation was the dominant contributor to overall prediction uncertainty accounting for 32% of the variation in final abundance (Table 14). Parameter estimation error was the next largest contributor accounting for 11%, while residual or unexplained variation in the population growth models was the least significant contributor accounting for 3% of the variation in final abundance.

Table 14. Variation in the final abundance of wild Sonoran pronghorn and percent reduction due to the removal of each component. Results are for the management scenario including the reestablishment of an additional wild population and including immigration from the captive population.

Component of uncertainty removed	Variation included in viability model	Variance in final abundance	Percent reduction in all-sources variance
	All sources	8628	
Future precipitation	Parameter estimation and model residual	5886	32
Parameter estimation	Model residual and future precipitation	7644	11
Model residual	Future precipitation and parameter estimation	8341	3

Implications

Cressie et al. (2009:553) recently stated, "The field of ecology is becoming increasingly aware of the importance of accurately accounting for multiple sources of uncertainty when modeling ecological phenomena and making inferences. … However, accounting for various sources of uncertainty is by no means a simple task." Despite recognition of the importance of incorporating various sources of uncertainty into PVA (Reed et al. 2002), the complexity of PVA models seemed to have precluded robust attempts to include multiple sources of uncertainty into predictions (but see Bakker et al. 2009 for a recent exception). We presented an approach for accomplishing this goal for PVA models based on time-series of abundance data. Our approach was similar to that used by Bakker et al. (2009) in that each source of uncertainty was quantified based on empirical data and then propagated within the projection model. By doing so, we were able to more realistically evaluate the benefit of the captive breeding program and potential reestablishment of an additional wild population to Sonoran pronghorn viability. Additionally, we were able to identify which source (i.e., future precipitation) was the greatest contributor to overall uncertainty such that future research could target this source to acquire more confidence in future predictions.

As expected, including more sources of uncertainty resulted in more ambiguous conclusions regarding the benefit of the captive population at CPNWR and the reestablishment of an additional wild population on BMGR-East. While the relative benefit of each management

option was evident from deterministic projections, incorporation of major sources of uncertainty revealed additional insight about the expected fate of Sonoran pronghorn under these management options. For example, deterministic projections suggested the wild population without immigration from the captive breeding program would undergo a slight decline in abundance from 34 to 26 females over the next 20 years. However, when uncertainty was included, the most likely final abundance was much lower (i.e. <10; see Figure 36). Additionally, there was considerable uncertainty in the final abundance of the wild population with immigration and the reestablishment of an additional population as evidenced by the relatively flat probability distribution for final abundance (see Figure 36). However, despite this increased uncertainty, both management actions (i.e., the captive population at CPNWR and the reestablishment of an additional wild population) dramatically increase the viability of wild Sonoran pronghorn. Without the additional individuals provided by the captive breeding program, the wild population has a high probability of reaching abundance levels that are unsustainable and a low probability of reaching an abundance that is higher than 100 females.

The dominant contributor to overall uncertainty in future abundance of Sonoran pronghorn was the lack of knowledge of future precipitation. Two factors are responsible for this relationship. First, there was a close association between Sonoran pronghorn population growth and the amount of biennial precipitation. Thus, future abundance of Sonoran pronghorn was closely tied to future precipitation. The second factor was highly variable biennial precipitation (i.e., coefficient of variation = 0.33). Thus, approximately 90% of the simulated values for future precipitation would range from 4.2 to 20.4 inches, a range that would dramatically influence population growth (see Figure 27) and result in highly variable future population abundances. It is worth noting that even though precipitation was the dominant source of uncertainty, there is actually *more* uncertainty than our simulations suggest. For example, we did not include error from our estimates of mean and standard deviation of biennial precipitation. Furthermore, there is likely substantial model selection uncertainty related to projecting future precipitation. In sum, research will need to make modeling future precipitation a high priority.

In comparison to uncertainty in future precipitation, parameter estimation error contributed less to overall uncertainty in future pronghorn abundance. Our results suggest that removal of parameter estimation error would reduce overall uncertainty by 11%. While this reduction is not negligible, it is surprisingly small considering the limited data from which model parameters were estimated (sample sizes of 5 for the captive population and 8 for the wild population). Nonetheless, there are two ways future research could reduce this uncertainty. The first, and most obvious, is to collect more data. Thus, to reduce prediction uncertainty due to estimation error, it will be important to continue current monitoring efforts. In particular, the number of adult females and female offspring of these individuals in the captive population(s) will need to be recorded annually. It is equally important to continue to obtain biennial estimates of abundance for the wild population. Related, a better estimate of the sex ratio in the wild population would allow for a closer match between model predictions and actual female

abundance. A second, less obvious, way to reduce estimation error is to develop better models of population growth. Reducing the residual or unexplained variation in population growth models has the dual benefit of both reducing uncertainty due to this source as well as reducing parameter estimation error. So while residual error was the least significant contributor to overall prediction uncertainty, future research should continue to seek ways to reduce unexplained variation in Sonoran pronghorn growth rates. For example, there are several factors (e.g., predator abundance, supplemental feeding or watering, forage abundance/quality, etc.) that could be included as potential covariates in models of population growth. Incorporating these additional covariates will necessarily lead to increased parameter estimation error or model variance but if information-theoretic criteria are used for model selection, there is a good chance that additional covariates will only be included if the reduction in residual variation (i.e., model bias) outweighs the increase in model variance.

Our main goal was to develop an approach for including most of the dominant sources of uncertainty into PVA models based on time-series of abundance data. However, our demonstration of this approach using Sonoran pronghorn makes this research highly relevant to DoD and BMGR. We demonstrated that there is significant value to the reestablishment of an additional wild population of Sonoran pronghorn on BMGR-East as well as the maintenance of the current captive breeding program at CPNWR. Now that the approach has been developed, we encourage further application by DoD to assess management scenarios not included in our analysis. For example, the most ambitious alternative for reestablishment proposed by USFWS (2009) calls for the creation of an additional captive population on Kofa National Wildlife Refuge (KNWR) and the reestablishment of a 3rd wild population north of the current distribution on KNWR. We see great potential to include our approach within an optimized decision process to determine how long these captive programs will need to be maintained (e.g., Schuab et al. 2009) and to evaluate other management options.

CONCLUSIONS AND IMPLICATIONS: AN EXPANDED TOOLSET FOR ASSESSING MANAGEMENT OF LISTED SPECIES ON DEPARTMENT OF DEFENSE LANDS

Military managers and biologists are frequently faced with evaluating how a wide range of activities may affect the viability of species of concern. In the previous sections we described three approaches, with accompanying tools for implementation, to evaluate these effects that can be applied given the widely varying levels of data availability typically encountered by biologists. The first is a framework based on structured population models that can be used to evaluate the effect management actions might have on population growth rate for species about which little is known. The approach leverages information on how particular management actions affect the demographic vital rates of either the focal species or similar surrogate species to determine the conditions under which a positive growth rate can be expected. This framework is especially helpful for developing a course of immediate action to prevent further decline and prioritizing future research and management. As an example, we demonstrated that arroyo toad population growth is highly dependent on survival of toads during their terrestrial life stages (adult and juvenile). We also illustrated the strong effect of parameter uncertainty on population persistence estimates, underscoring the need to obtain better measures of survival in this species. Other forms of uncertainty have similarly strong influences on population growth in other species. When we incorporated environmental variability into a meta-analysis of management effects on plant vital rates, we found that the effectiveness of specific management activities varied depending on the type of habitat and the life stages targeted by the management actions. Again, these results drive home the importance of identifying the most influential sources of uncertainty and undertaking efforts to better estimate those parameters.

The second approach makes use of commonly available abundance estimates that have been collected over a period of years. These time series of count data are the product of long-term monitoring programs and can be used to fit various stochastic models of population growth which can then be used to assess population trend and viability or identify important environmental drivers of population growth. Publicly available software (PopGrowth) was created to facilitate these analyses. In addition, we extended exponential and density-dependent state space models, which include both environmental process variability and observation error, to accommodate data sets with missing time intervals. These models greatly enhance the ability of researchers to assess the influence of density dependence, environmental covariates, and sampling error on population growth, even when time series of abundance estimates are incomplete. We applied a set of population growth models to the greater sage-grouse population at Yakima Training Center (YTC) and showed that the population growth rate is negatively influenced by drought and increasing area of grassland habitat. Overall, the probability of this population dropping below an extinction threshold of 50 lekking males was high under the models that incorporated drought or grassland area. This analysis illustrates the importance of

managing for native shrubland habitat but also suggests that continued persistence of the YTC sage-grouse population may require management intervention beyond habitat preservation.

Third, for the few, albeit important, species for which there is detailed information about vital rates, spatial structure, and metapopulation characteristics, we developed methods and software for conducting global sensitivity analyses of viability models for single or multiple populations. Results from these sophisticated sensitivity analyses can be used to identify the relative effects of various management decisions on species viability as well as identifying the parameters that need to be estimated more precisely to reduce model uncertainty. We demonstrated these analyses using a pilot conservation incentive program for the golden-cheeked warbler at Fort Hood. We found that uncertainty in model structure and parameter estimates made it impossible to develop general guidelines for valuing golden-cheeked warbler habitat patches, and identified parameters that need to be targeted in future research.

Finally, we combined several of these approaches to incorporate various sources of uncertainty into population viability models, using the Sonoran pronghorn at Barry M. Goldwater Range as an example. Using time-series estimates of abundance for multiple populations, we estimated the probability of persistence for Sonoran pronghorn under 3 management scenarios and identified the sources of uncertainty that most need to be reduced to improve projections of persistence under different management actions. Despite the inclusion of all major sources of prediction uncertainty, our results showed a clear and substantial benefit, in terms of overall viability, to supplementing the wild population with individuals from the captive population at Cabeza Prieta National Wildlife Refuge.

While the demonstrations of our approaches have clear and immediate use to the managers of focal installations, our work has implications beyond the specific case studies presented here. The tools we've developed can guide management and research priorities regardless of the amount or type of information known about a species of concern. They can make informed evaluations of how a population is doing and what might be the effects of different types of management. With these approaches, assumptions and uncertainty about model structure and parameter estimates are more explicit, allowing for critical evaluation of model results. Perhaps most importantly, each of these tools provides direction as to how future research should proceed by elucidating the factors that are most important to population viability.

The basic premise behind each of our tools is that we can evaluate the effect of management actions by employing various methods of uncertainty and sensitivity analysis to an appropriate model of population growth. Critical to effective implementation is knowledge of how management actions affect particular parameters in a population growth model. The approaches developed here can be applied in an adaptive management framework to guide science-based recovery actions across a range of available data and management actions. This is a great opportunity for adaptive management to provide the empirical knowledge that is vital to the success of population viability models.

Future Directions

The goal of our project was to develop methods and tools for evaluating the effects of management or training on the viability of listed species based on the level of biological information known. Throughout our work we have recognized the challenges presented by uncertainty in model predictions. If overall uncertainty in model predictions is too large, inferences about changes in population viability due to management or military actions will be unreliable. To effectively isolate these effects, we must first quantify overall uncertainty, partition the uncertainty into contributions from each component, and then reduce the uncertainty. Our project has set the foundation for achieving this goal by demonstrating approaches for quantifying and partitioning different sources of uncertainty. Further development of this work would include finding ways to reduce sources of uncertainty through an iterative process of adaptive management. Adaptive management, although easily described (i.e., 'learning by doing'), can be challenging to implement particularly in the context of marrying hard-won field data with rigorous population ecology models to recover species. When implemented in an adaptive management framework, our approaches for quantifying sources of uncertainty can be used to focus research and monitoring efforts so field data can be efficiently gathered and incorporated into an analysis of population viability.

Technology Transfer

Key to the success of this project was the engagement of DoD biologists and managers in the framing of questions and development of databases and analytical software. This was accomplished by hosting workshops and informational sessions at installations where focal species occur, hosting workshops at national conferences, and presenting posters and oral presentations at national meetings of DoD biologists and managers. Details of workshops, presentations, and publications are provided in Appendix B.

As we prepared to apply each of our tools to species of DoD management concern, we met with natural resources staff from installations hosting populations of potential focal species. These meetings helped identify ongoing management questions for these species, identify and gather available data for each species, assess the suitability of our approaches for each species, and introduce our approaches to DoD biologists. During this phase we met with staff from Fort Hood, YTC, BMGR, Fort Huachuca, Mountain Home Air Force Base, Eglin Air Force Base, Camp Roberts/Camp San Luis Obispo, and Fort Hunter Liggett. These meetings often included agency and collaborating biologists (e.g., USFWS, The Nature Conservancy, Texas A&M University). We later hosted an installation-specific workshop at YTC to demonstrate the analyses and software we had developed and present preliminary results of our population viability analyses for sage-grouse at YTC.

We organized workshops at national meetings where we introduced our approaches for population viability analysis to biologists and managers. These events included a workshop at The Wildlife Society national conference in Miami, Florida in 2008 and a technical session and workshop at the National Military Fish and Wildlife Association conference in Washington, D.C in 2009. Additionally, we coordinated technical sessions at The Wildlife Society national conference in Monterey, California in 2009 and the SERDP-ESTCP Technical Symposium in 2008, each of which brought together experts in endangered species management to discuss challenges and perspectives on post-recovery management of listed species.

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APPENDICES

Appendix A. Supporting Data

General life history models with selected results

Appendix B. Scientific Publications

Scientific Publications

Workshops at National Professional Conferences

Site-Specific Conferences

Presentations at Scientific Meetings and Conferences

Workshop Materials

Appendix C. Other Supporting Materials

PopGrowth: Installation and Tutorial

R code for density dependent state space model for population abundance data with unequal time intervals

Source R code for fitting population growth models and projecting future Sonoran pronghorn viability

Appendix A. Supporting Data

General life history models with selected results

Many threatened and endangered species on Department of Defense lands share similar life history traits (e.g. annual and biennial plants, amphibians, birds that mature in their first year). In this appendix we include models for eight general life history types commonly found on DoD installations, and demonstrate how, for each life history type, population growth rates are predicted to change as function of changes to mean demographic rates, and with increasing variability in these rates. Any particular species would be a specific case of one of these models.

Included are the following models:

1) annual plants
2) semelparous perennial or biennial plants
3) perennial plants
4) amphibians
5) birds maturing at 1 year of age
6) slow maturing, long-lived birds
7) slow maturing, long-lived turtle
8) small mammals (e.g. mice, kangaroo rats)

1) A general model for annual plants
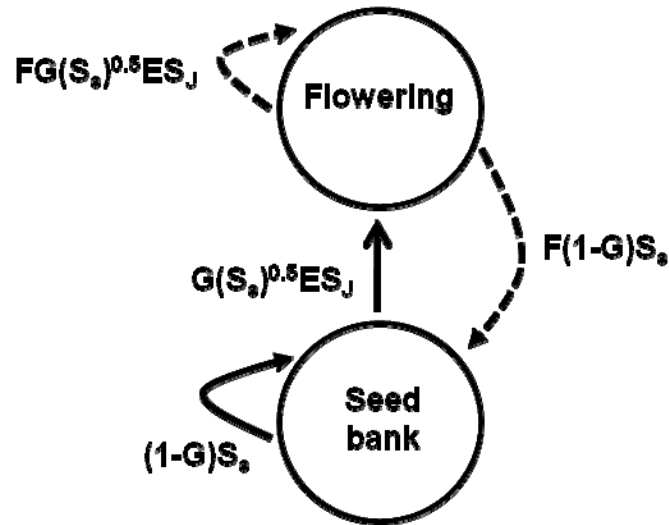
Figure A-1: A life cycle diagram encapsulating the basic life history of an annual plant.

$$\begin{bmatrix} (1-G)S_S & F(1-G)S_S \\ \sqrt{S_S}\,GES_J & F\sqrt{S_S}\,GES_J \end{bmatrix}$$

Figure A-2: A general matrix model for an annual plant.

Table A-1: Parameter definitions and values used in the annual plant model.

Parameter	Values used	Definition
F	1 - 200	number of viable seeds produced per plant
S_s	0.3, 0.6	annual seed survival
G	0.5	probability a seed germinates
E	0.05 – 1.0	probability a germinated seed becomes a seedling
S_j	0.3, 0.6, 0.9	survival from seedling stage to flowering
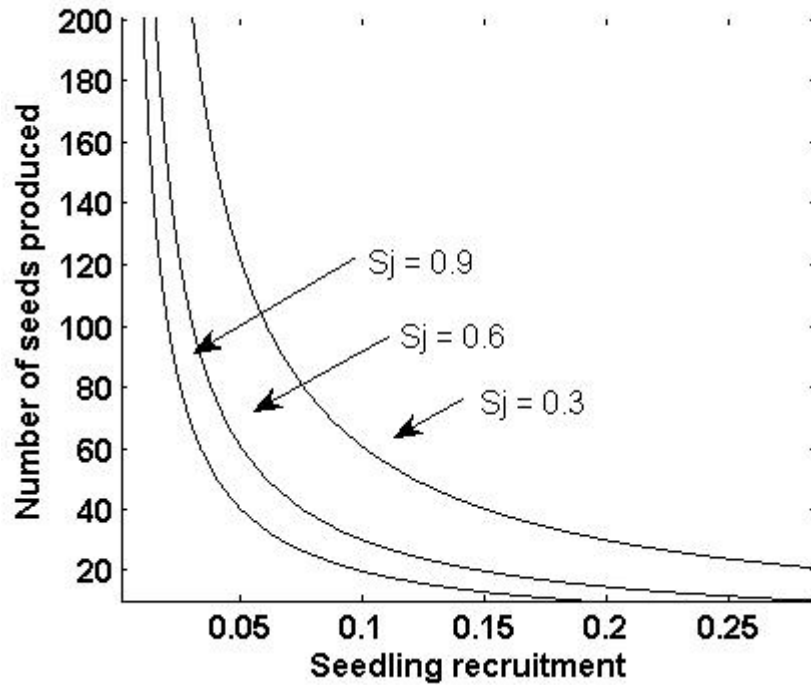
Figure A-3: Output of a deterministic matrix model for an annual plant. Mean annual seed survival (Ssd) is kept constant at 60%, while the three lines represent output from models in which mean survival from the seedling stage to reproduction (Sj) is 30%, 60% and 90%.
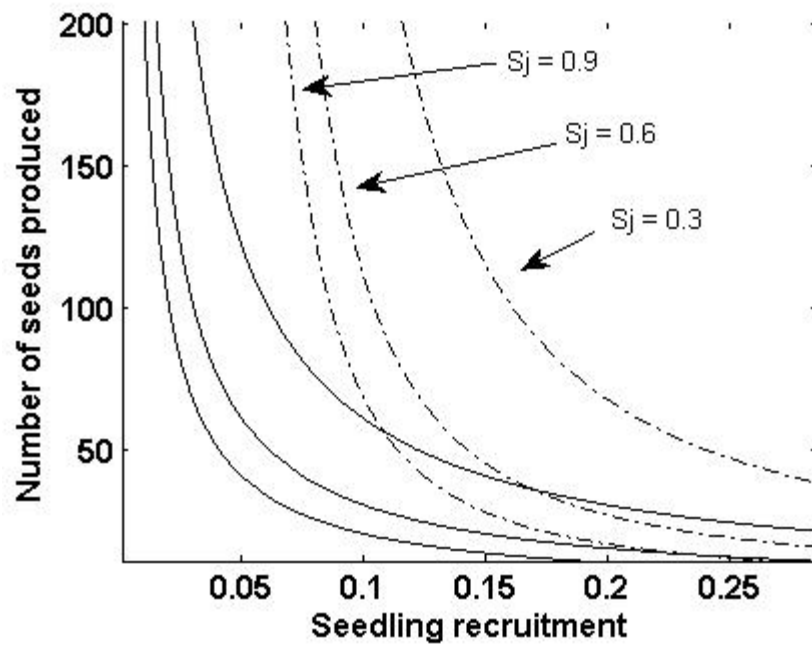
Figure A-4: Output of a stochastic matrix model (dashed lines) for an annual plant when all parameters vary at 25% of their maximum possible σ values. Mean annual seed survival (Ssd) is kept constant at 60%, while the three lines represent models in which mean survival from the seedling stage to reproduction (Sj) is 30%, 60% and 90%. Solid lines represent the results from the deterministic model (as in Figure A-3).
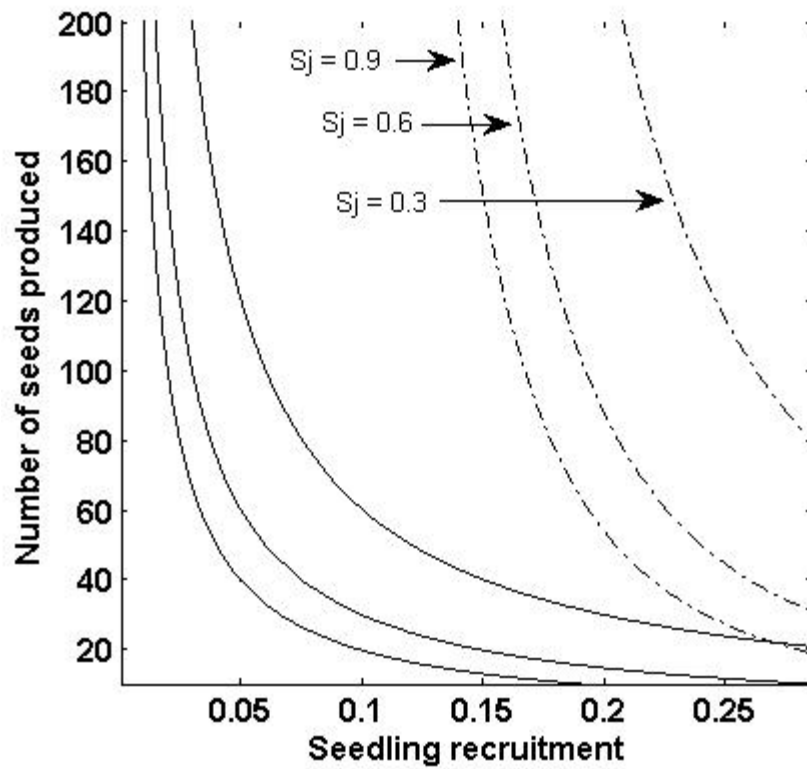
Figure A-5: Output of a stochastic matrix model (dashed lines) for an annual plant when the number of seeds produced per plant (F) and seedling recruitment (E) vary at 75% of their maximum possible σ value, while all other parameters vary at 25% of their maximum σs. Mean annual seed survival (Ssd) is kept constant at 60%, while the three lines represent models in which mean survival from the seedling stage to reproduction (Sj) is 30%, 60% and 90%. Solid lines represent the results from the deterministic model (as in Figure A-3).
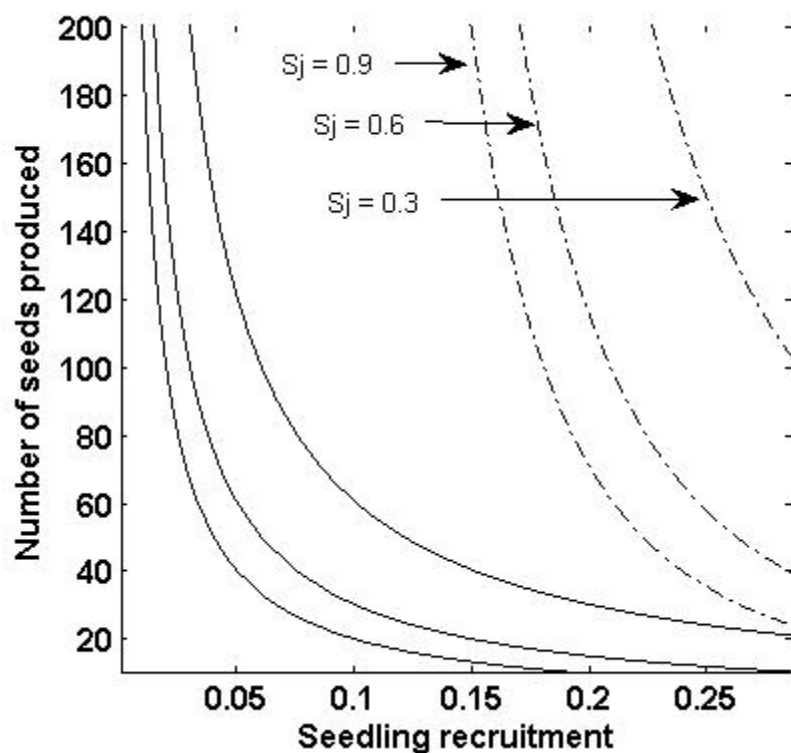
Figure A-6: Output of a stochastic matrix model (dashed lines) for an annual plant when the number of seeds produced per plant (F), germination rate (G) and seedling recruitment (E) vary at 75% of their maximum possible σ values, while all other parameters vary at 25% of their maximum σs. Mean annual seed survival (Ssd) is kept constant at 60%, while the three lines represent models in which mean survival from the seedling stage to reproduction (Sj) is 30%, 60% and 90%. Solid lines represent the results from the deterministic model (as in Figure A-3).
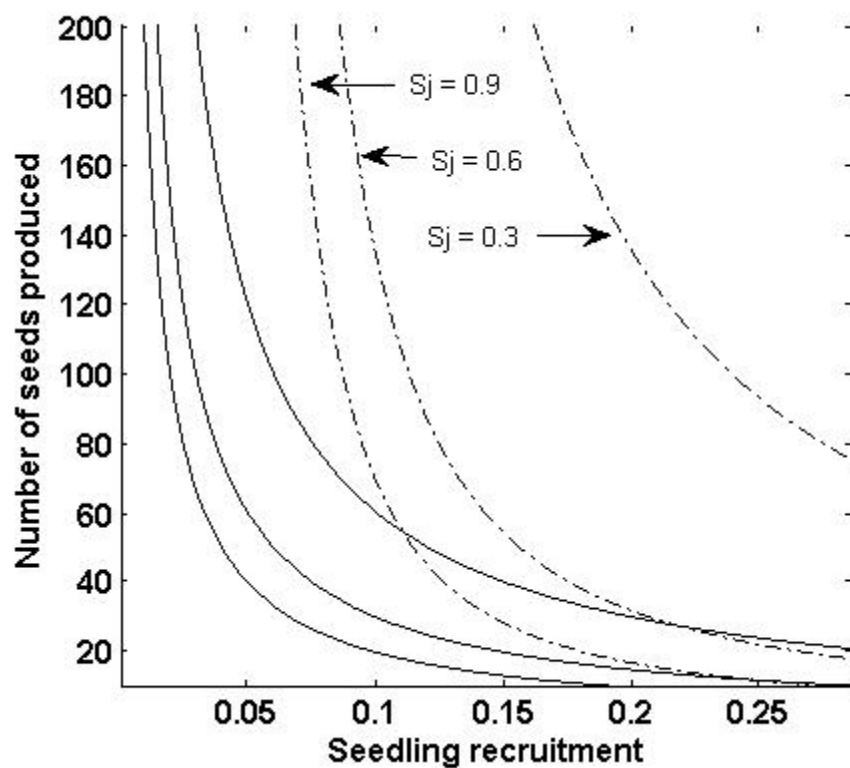
Figure A-7: Output of a stochastic matrix model (dashed lines) for an annual plant when just the survival from seedling to reproduction (Sj) varies at 75% of its maximum possible σ values, while all other parameters vary at 25% of their maximum σs. Mean annual seed survival (Ssd) is kept constant at 60%, while the three lines represent models in which mean survival from the seedling stage to reproduction (Sj) is 30%, 60% and 90%. Solid lines represent the results from the deterministic model (as in Figure A-3).
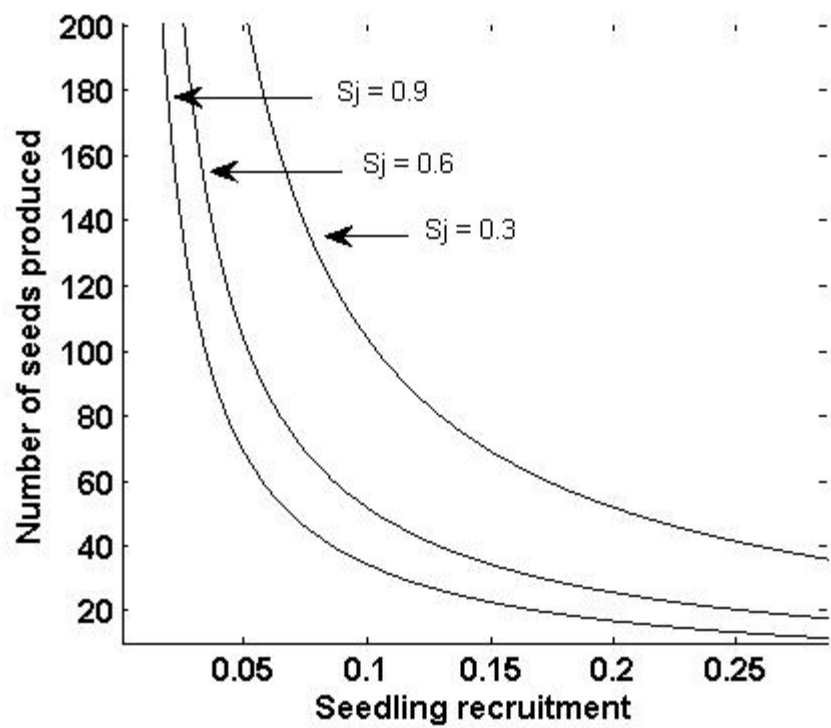
Figure A-8: Output of a deterministic matrix model for an annual plant when mean survival from seedling to reproduction (Sj) is 30%, 60% and 90% and mean annual seed survival is 30%.
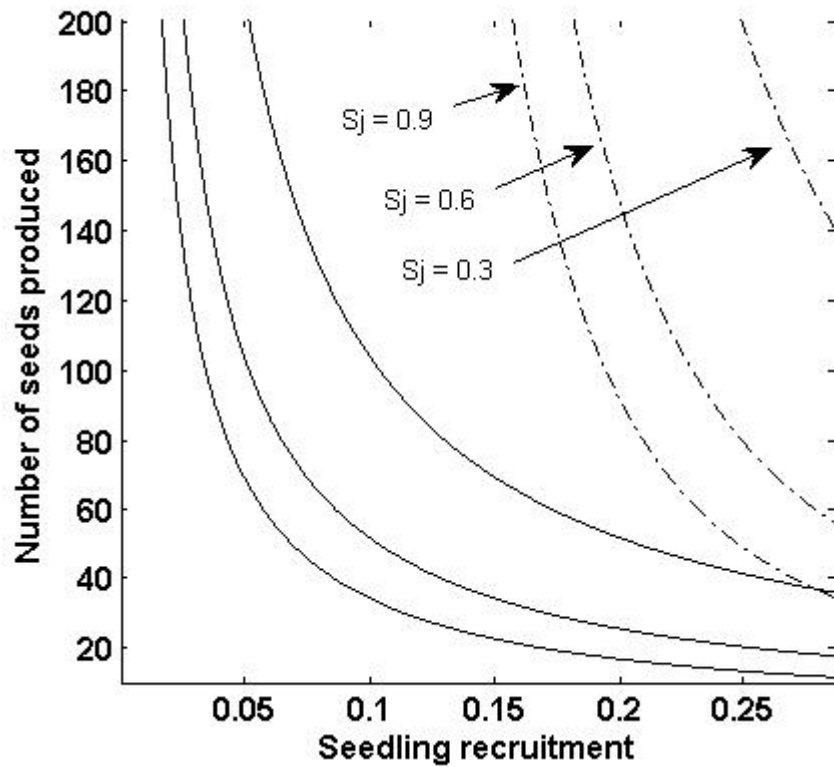
Figure A-9: Output of a stochastic matrix model (dashed lines) for an annual plant when the number of seeds produced per plant (F) and seedling recruitment (E) vary at 75% of their maximum possible σ values, while all other parameters vary at 25% of their maximum σs. Mean annual seed survival (Ssd) is kept constant at 30%, while the three lines represent model output in which mean survival from the seedling stage to reproduction (Sj) is 30%, 60% and 90%. Solid lines represent the results from the deterministic model (as in Figure A-8).
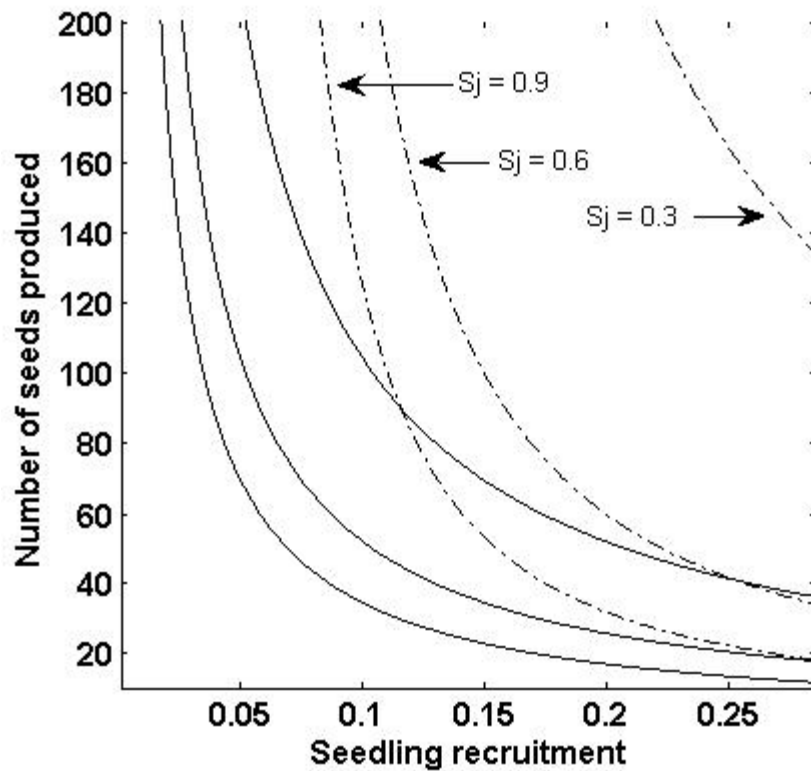
Figure A-10: Output of a stochastic matrix model (dashed lines) for an annual plant when just the survival from seedling to reproduction (Sj) varies at 75% of its maximum possible σ value, while all other parameters vary at 25% of their maximum σs. Mean annual seed survival (Ssd) is kept constant at 30%, while the three lines represent models in which mean survival from the seedling stage to reproduction (Sj) is 30%, 60% and 90%. Solid lines represent the results from the deterministic model (as in Figure A-8).

2) A general model for biennial/semelparous perennial plants
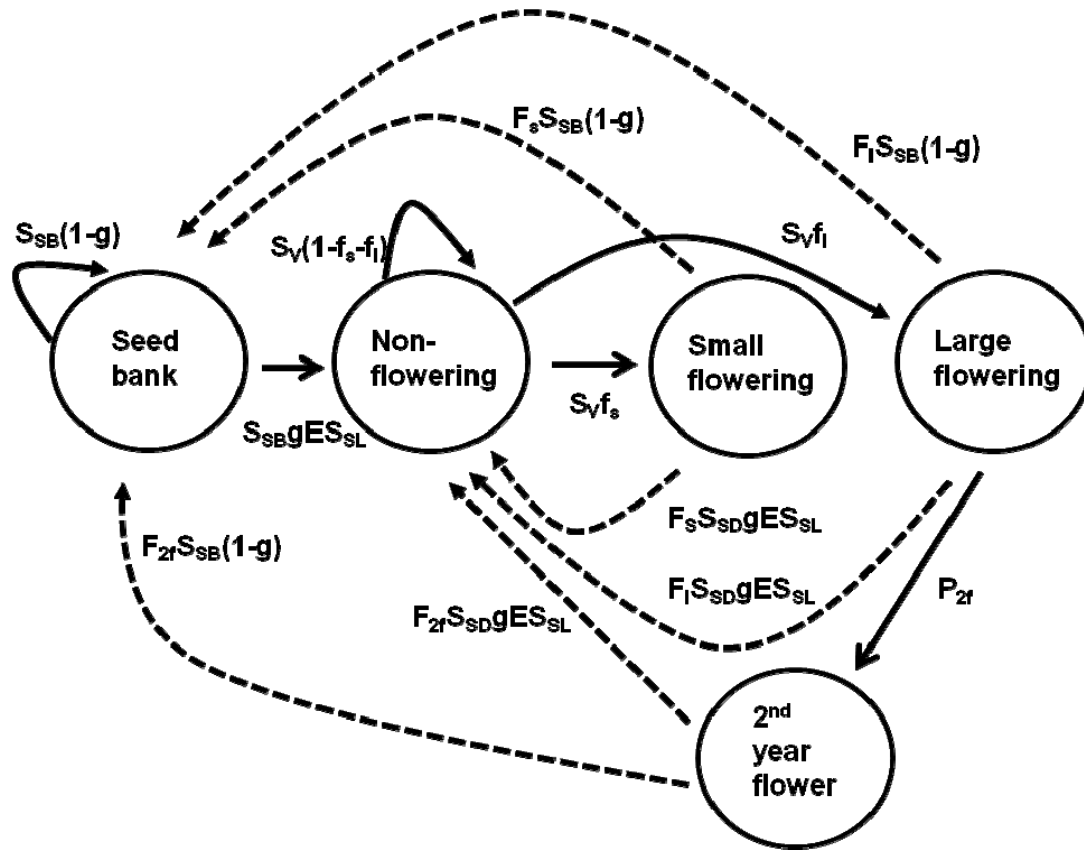
Figure A-11: A life cycle diagram encapsulating the basic life history of a biennial/semelparous perennial plant.

$$
\begin{bmatrix}
S_{sb}(1-g) & 0 & F_s S_{sb}(1-g) & F_l S_{sb}(1-g) & F_{2f} S_{sb}(1-g) \\
S_{sd} g ES_{SL} & S_v(1-f_S-f_l) & F_s S_{sd} g ES_{SL} & F_l S_{sd} g ES_{SL} & F_{2f} S_{sd} g ES_{SL} \\
0 & S_v f_s & 0 & 0 & 0 \\
0 & S_v f_l & 0 & 0 & 0 \\
0 & 0 & 0 & P_{2f} & 0
\end{bmatrix}
$$

Figure A-12: A general matrix model for a biennial/semelparous perennial plant.

Table A-2: Parameter values and definitions for the biennial plant model representing the specific case of the Chorro Creek bog thistle.

Parameter	Values used	Definition
S_{sd}	0.1, 0.2, 0.4	survival of germinating seeds
S_{sb}	na	survival of seeds in seed bank
g	1.0	probability a seed germinates
$E*S_{SL}$	.001 – 0.3	probability a germinating seed successfully establishes and survives its first growing season
S_v	.01 – 0.96	probability a vegetative rosette survives to flower
f_s	0.6	probability of becoming a small flowering plant
f_l	0.2	probability of becoming a large flowering plant
p2f	0.01	probability of flowering for a second year
F_s	300	number of seeds produced per small flowering plant
F_l	600	number of seeds produced per small flowering plant
F_{2f}	300	number of seeds produced by plant in 2nd year
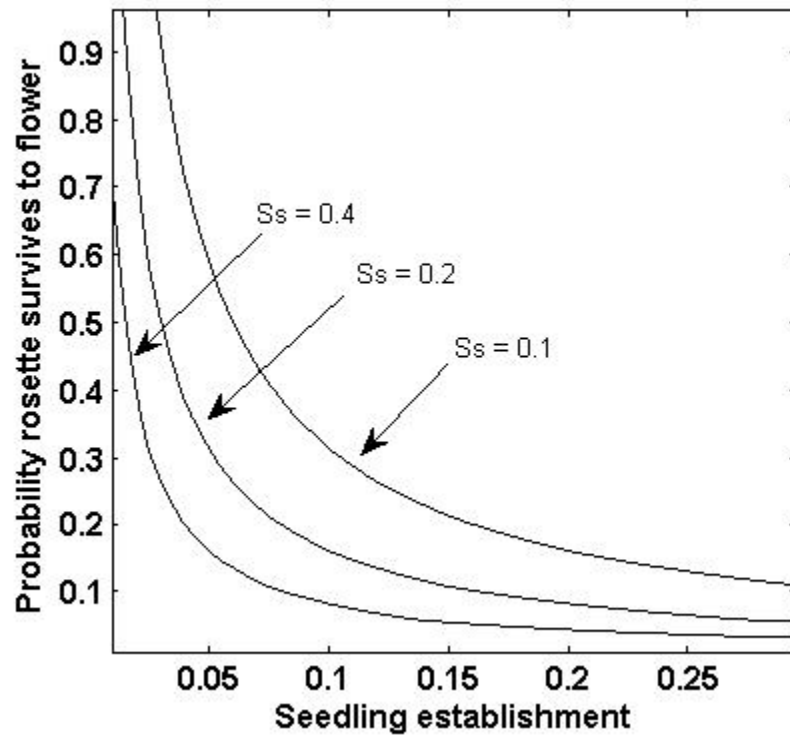
Figure A-13: Output of a deterministic matrix model for the Chorro Creek bog thistle using the parameters given in Table A-2. The three lines represent models runs with different values of seed survival (Ss) at 40%, 20% and 10%.
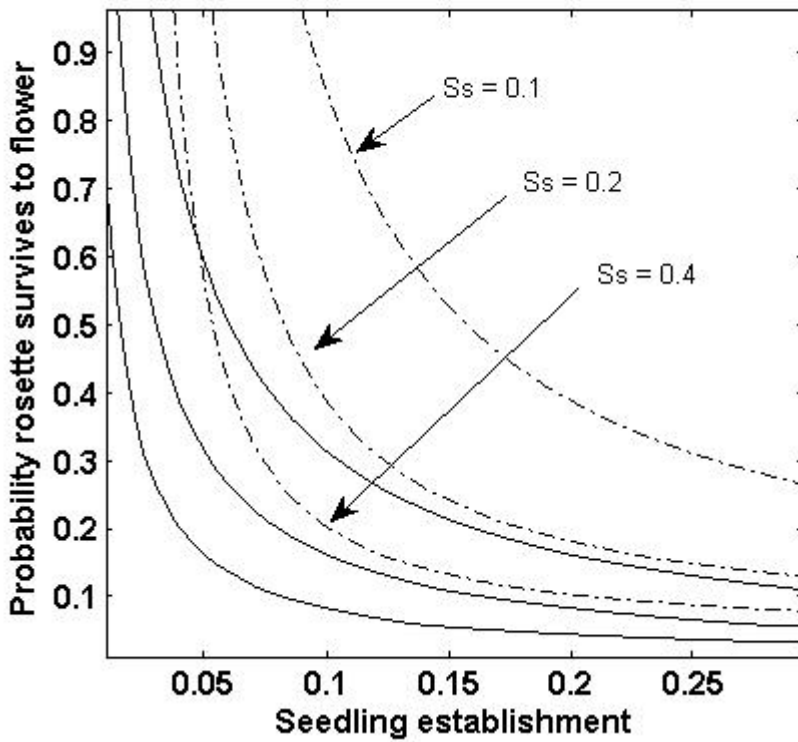
Figure A-14: Output of a stochastic matrix model (dashed lines) for the Chorro Creek bog thistle using the parameters given in Table A-2 in which all parameters values vary at 25% of their maximum σ values. The three lines represent models runs with different values of seed survival (Ss) at 40%, 20% and 10%. Solid lines are results from the deterministic model (as in Figure A-13).
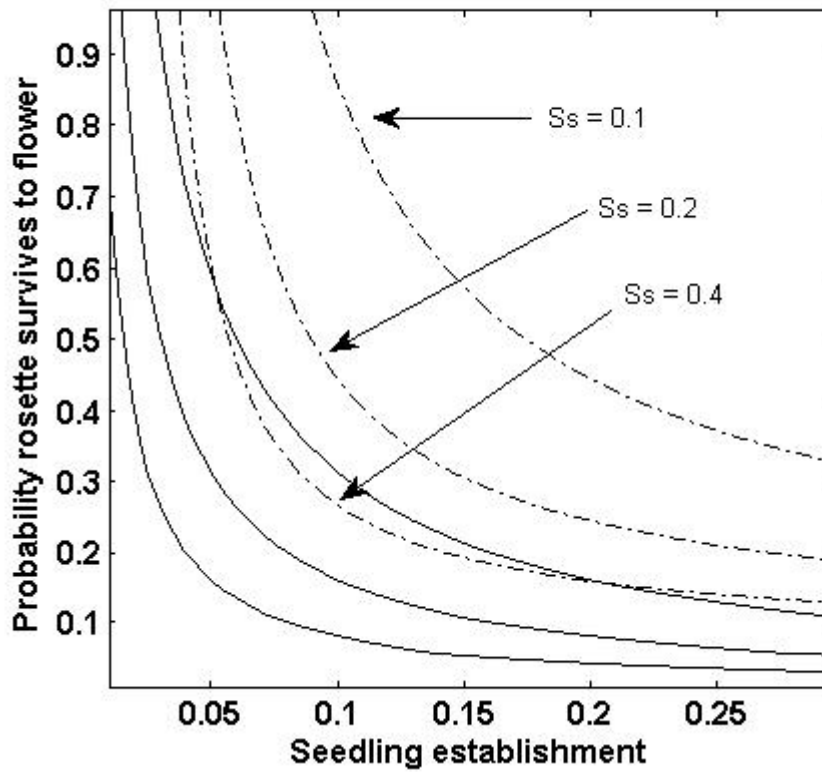
Figure A-15: Output of a stochastic matrix model (dashed lines) for the Chorro Creek bog thistle using the parameters given in Table A-2, with the probability a rosette survives to flower varying at 75% of its maximum σ, and all other parameters vary at 25% of their maximum σ values. The three lines represent model runs with different values of seed survival (Ss) at 40%, 20% and 10%. Solid lines are results from the deterministic model (as in Figure A-13).
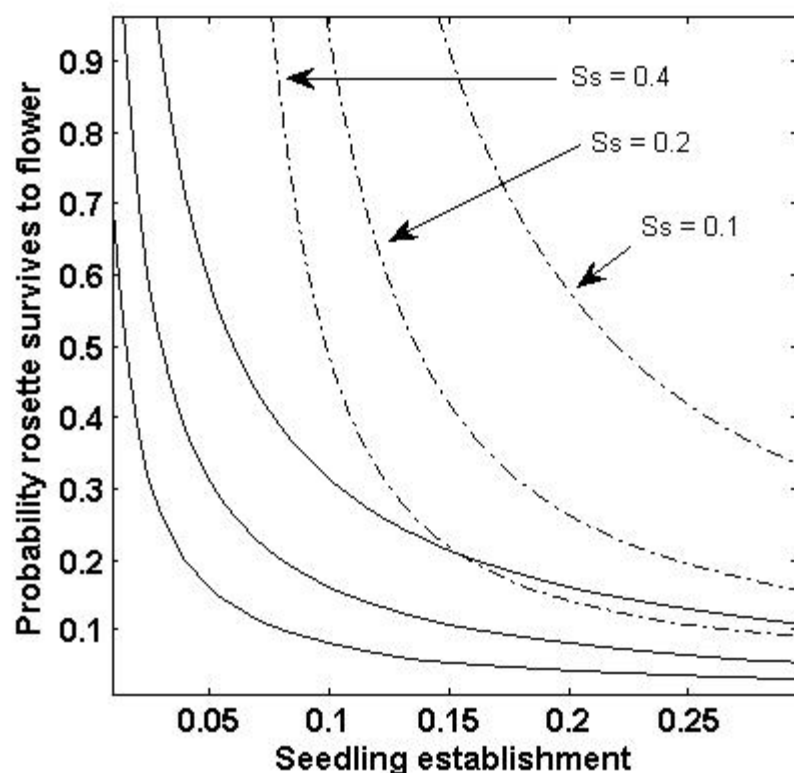
Figure A-16: Output of a stochastic matrix model (dashed lines) for the Chorro Creek bog thistle using the parameters given in Table A-2, with the number of seeds produced per flowering plant (F_i) and the probability a seed successfully establishes (E) varying at 75% of their maximum σ, and all other parameters vary at 25% of their maximum σ values. The three lines represent model runs with different values of seed survival (Ss) at 40%, 20% and 10%. Solid lines are results from the deterministic model (as in Figure A-13).

3) A general model for perennial plants
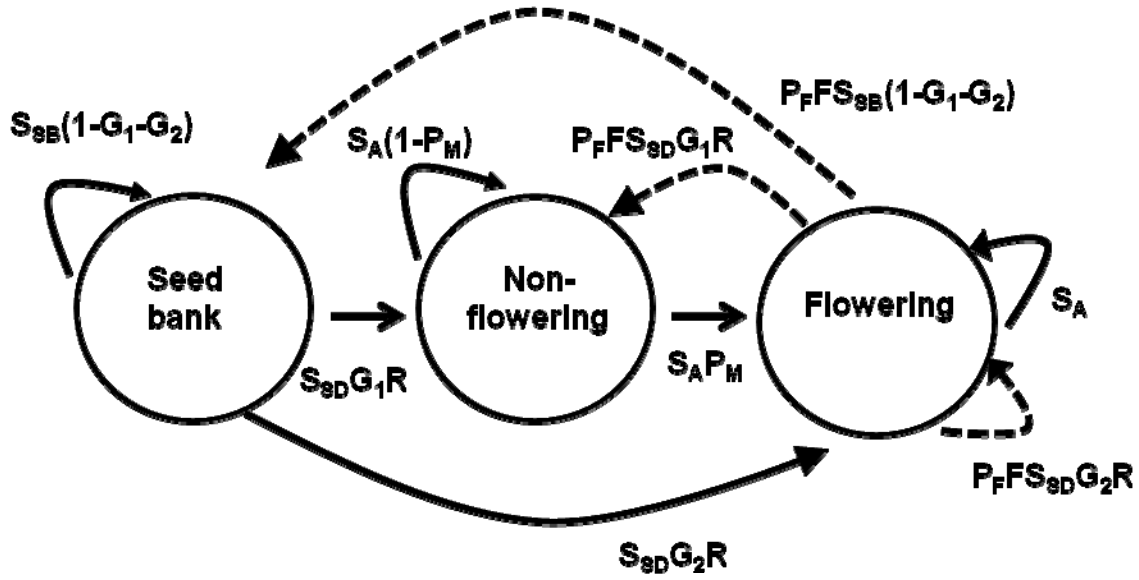
Figure A-17: Life cycle of a perennial plant.

$$
\begin{bmatrix}
S_{SB}(1-G_1-G_2) & 0 & P_F F S_{SB}(1-G_1-G_2) \\
S_{SD}G_1 R & S_A(1-P_M) & P_F F S_{SD}G_1 R \\
S_{SD}G_2 R & S_A P_M & S_A + P_F F S_{SD}G_2 R
\end{bmatrix}
$$

Figure A-18: Model of a perennial plant.

Table A-3: Parameter definitions and values used in the perennial plant model.

Parameter	Values used	Definition
F	10 - 200	number of viable seeds produced per plant
S_{SB}	0.5, 0.3, 0.2	survival of seed in seed bank
S_{SD}	$S_{SB}^{(1/2)}$	survival of germinating seeds
R	$0.001 - 0.29$	Probability of successful seedling recruitment
S_A	0.7, 0.9	annual survival of adult plant
P_M	0.3, 0.4	probability a vegetative plant becomes reproductively mature
P_F	0.8	probability a reproductively mature plant flowers
G_1	0.5	probability a germinating seed becomes a vegetative plant
G_2	0	probability a germinating seed becomes a reproductively mature plant

Model Output
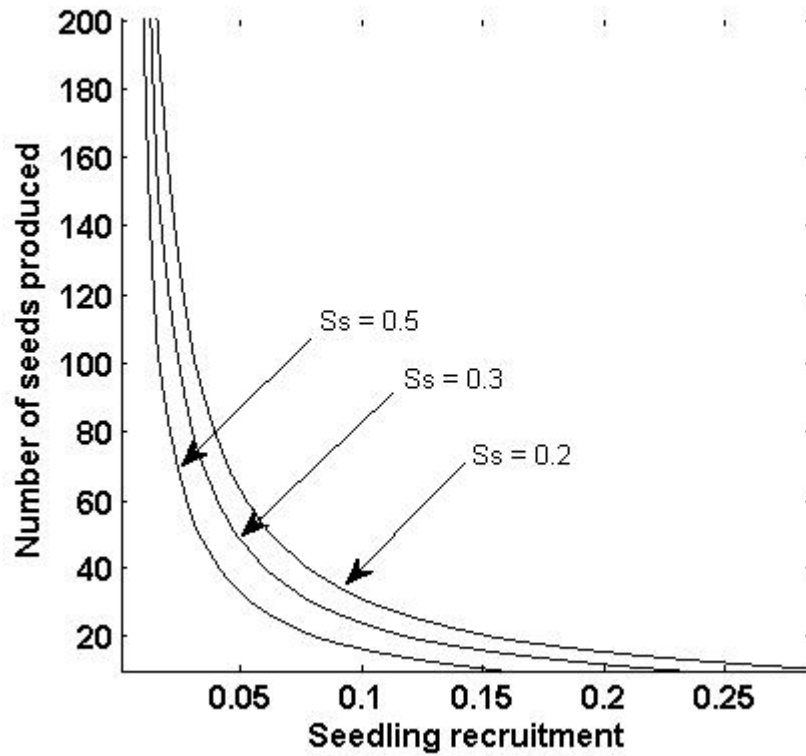
Figure A-19: Output of a deterministic, stage-structured model for a perennial plant using the parameters given in Table A-3. The three lines represent models runs with different values of seed survival (Ss) at 40%, 20% and 10%, the annual probability a vegetative plant becomes reproductively mature is 40% and annual survival of adult plants is 70%.
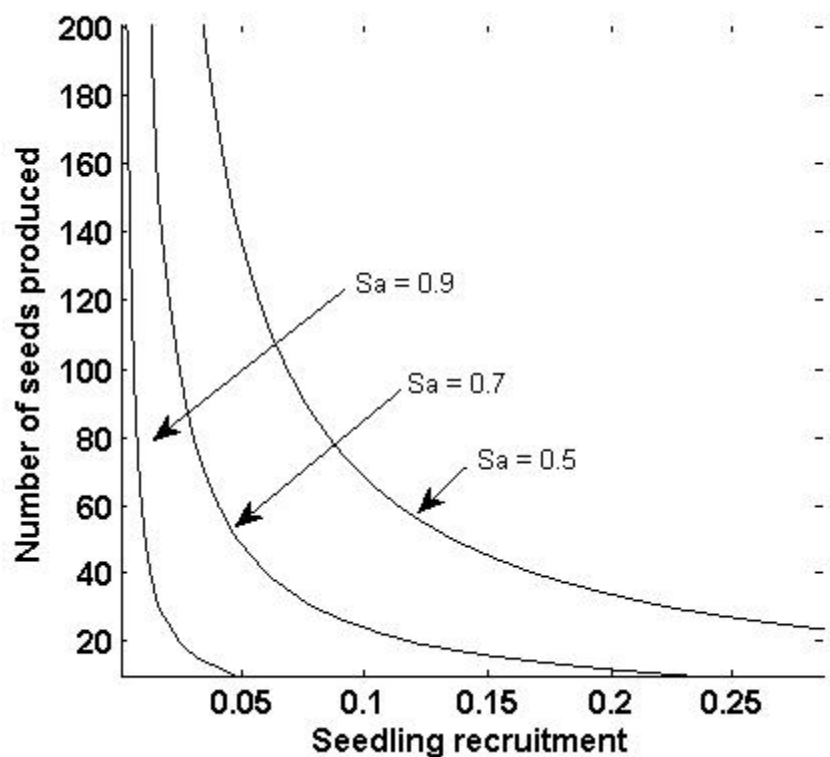
Figure A-20: Output of a deterministic, stage-structured model for a perennial plant using the parameters given in Table A-3. The three lines represent models runs with different values of annual adult survival (Sa) at 90%, 70% and 50%, the annual probability a vegetative plant becomes reproductively mature is 40% and annual seed survival is 30%.
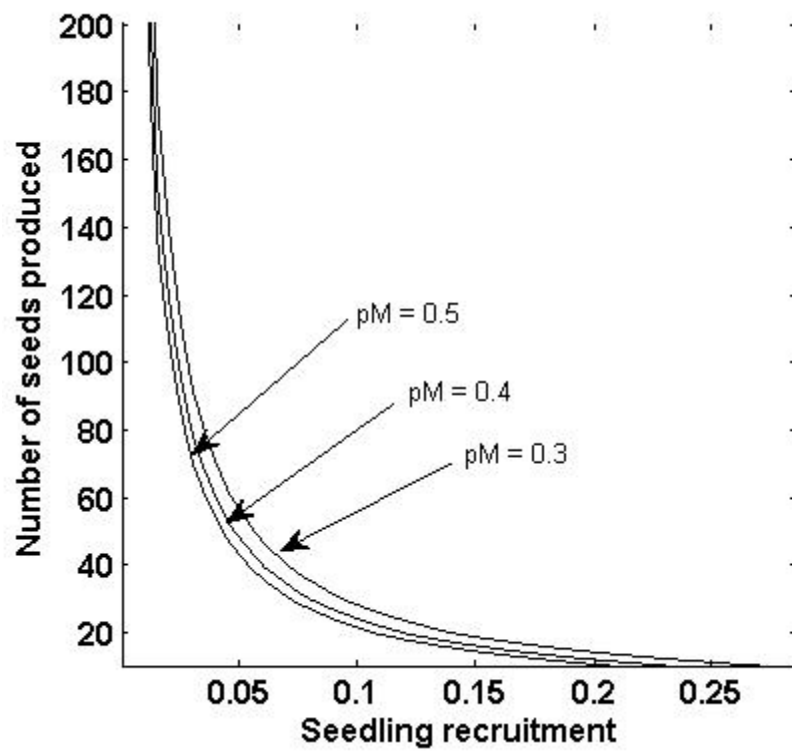
Figure A-21: Output of a deterministic, stage-structured model for a perennial plant using the parameters given in Table A-3. The three lines represent models runs with different values of the probability a vegetative plant becomes reproductively mature in any given year (pM) at 50%, 40% and 30%, the annual seed survival is 30% and annual adult survival is 70%.
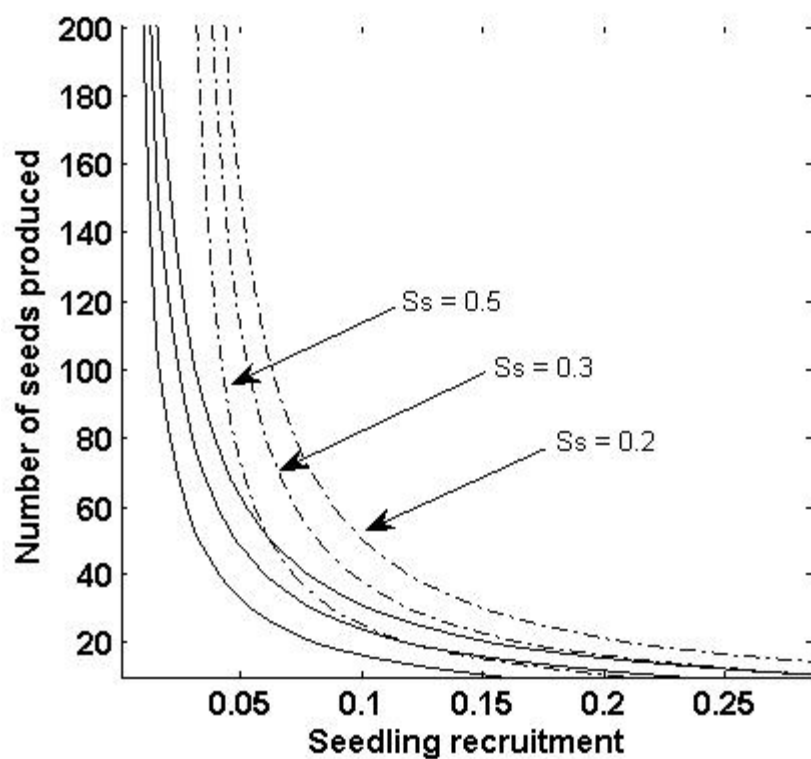
Figure A-22: Output of a stochastic, stage-structured matrix model (dashed lines) for a perennial plant using the parameters given in Table A-3, with all parameters varying at 25% of their maximum σ values. The three lines represent models runs with different values of seed survival (Ss) at 50%, 30% and 20%. Solid lines are results from the deterministic model (as in Figure A-19).
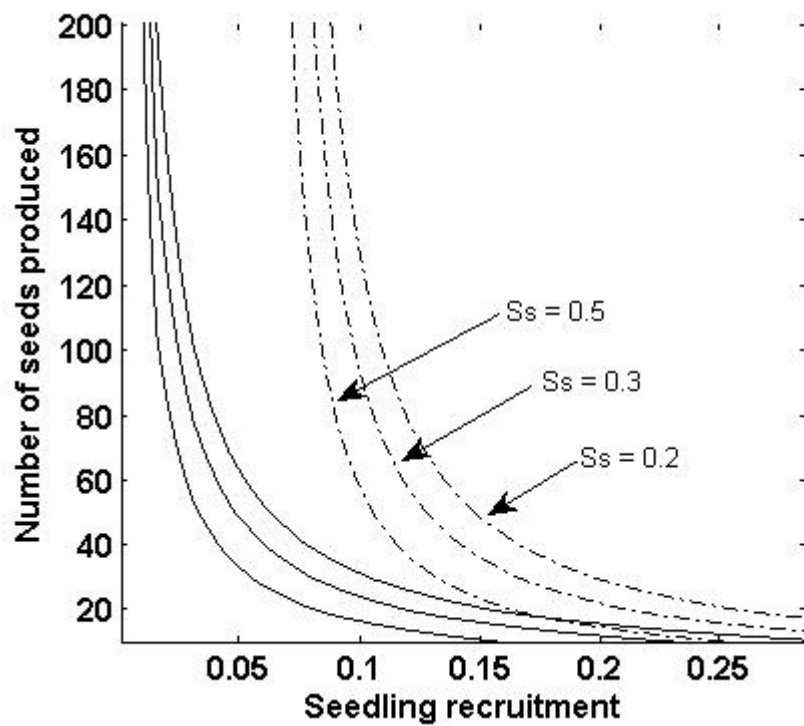
Figure A-23: Output of a stochastic, stage-structured matrix model (dashed lines) for a perennial plant using the parameters given in Table A-3, with the number of seeds produced per flowering plant (F), the probability a seed germinates (G_1), and the probability a seed successfully establishes (R) varying at 75% of their maximum σ values, and all other parameters vary at 25% of their maximum σ values. The three lines represent model runs with different values of seed survival (Ss) at 50%, 30% and 20%. Solid lines are results from the deterministic model (as in Figure A-19).
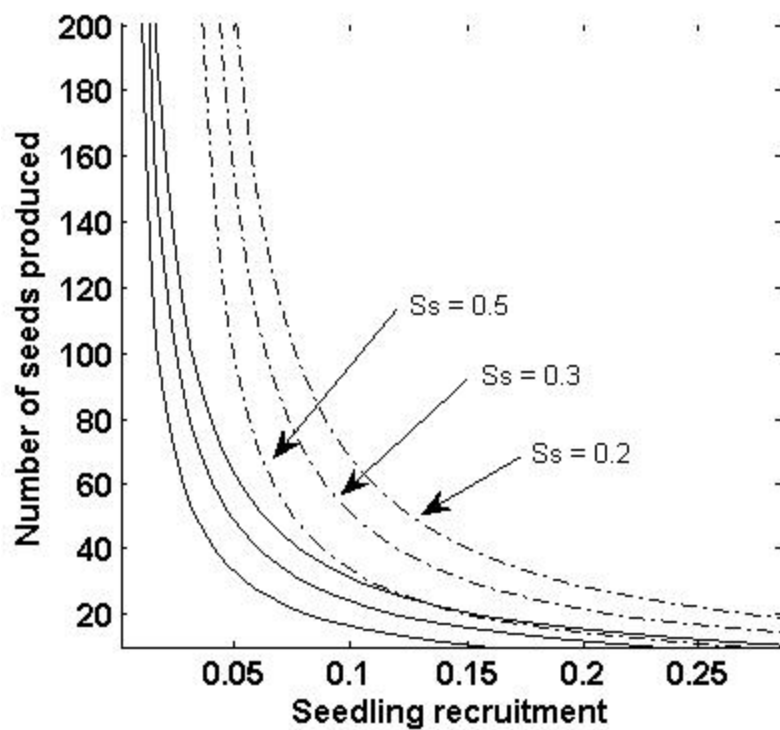
Figure A-24: Output of a stochastic, stage-structured matrix model (dashed lines) for a perennial plant using the parameters given in Table A-3, with annual adult survival (Sa) varying at 75% of its maximum σ value, and all other parameters vary at 25% of their maximum σ values. The three lines represent models runs with different values of seed survival (Ss) at 50%, 30% and 20%. Solid lines are results from the deterministic model (as in Figure A-19).

4) A general model for amphibians
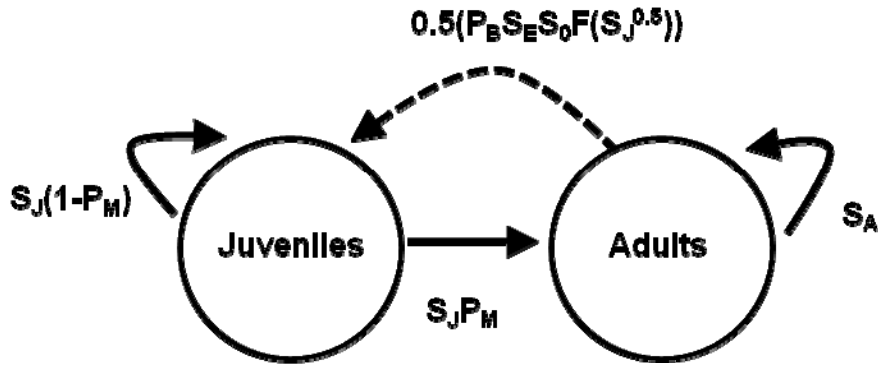
Figure A-25: General life cycle for an amphibian

$$\begin{bmatrix} S_J(1-P_M) & 0.5\left(P_B FS_E S_0 \sqrt{S_J}\right) \\ S_J P_M & S_A \end{bmatrix}$$

Figure A-26: General model of an amphibian

Table A-4: Parameter definitions and values used for the general amphibian model (based on the Flatwoods salamander, *Ambystoma cingulatum*).

Parameter	Values used	Definition
F	160	mean clutch size
P_B	0.4, 0.8	probability of breeding
S_E	0.75	egg survival
S_0	0.05 – 1.0	survival from egg to metamorph
S_J	0.05 – 1.0	annual juvenile survival
S_a	0.05 – 1.0	annual adult survival
P_M	0.25, 0.5, 0.75	probability juvenile becomes reproductively mature
(sex ratio)	0.5	sex ratio is 1:1
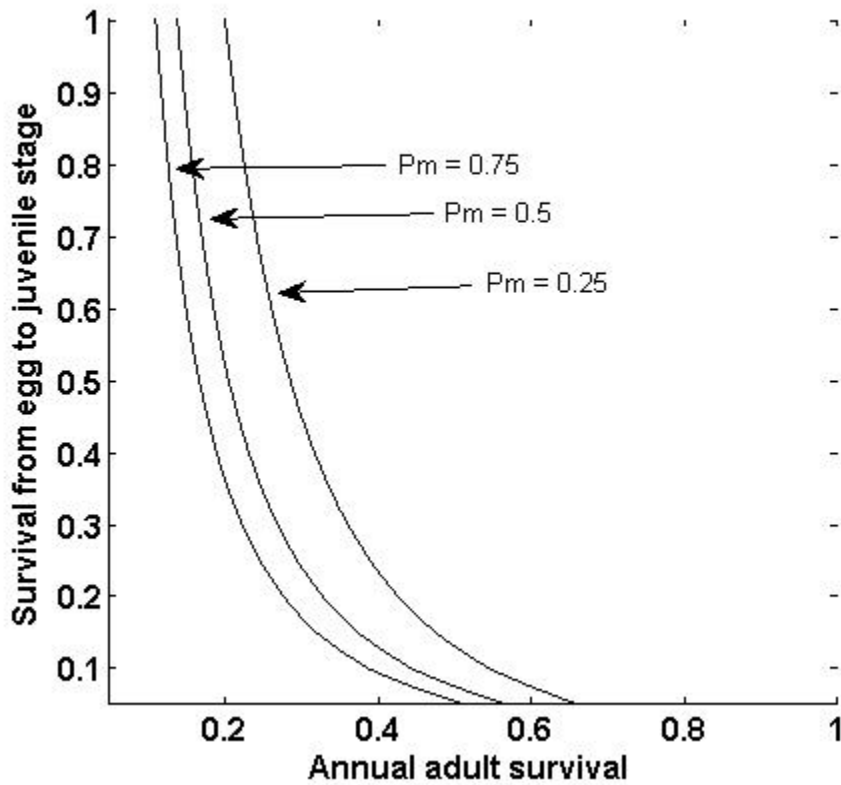
Figure A-27: Output of a deterministic matrix model for an amphibian using parameters given in Table A-4. The three lines represent different models in which the mean annual probability a juvenile becoming reproductively mature (Pm) is 75%, 50% and 25%, mean egg survival is 75%, and mean annual probability of breeding (Pb) is 80%.
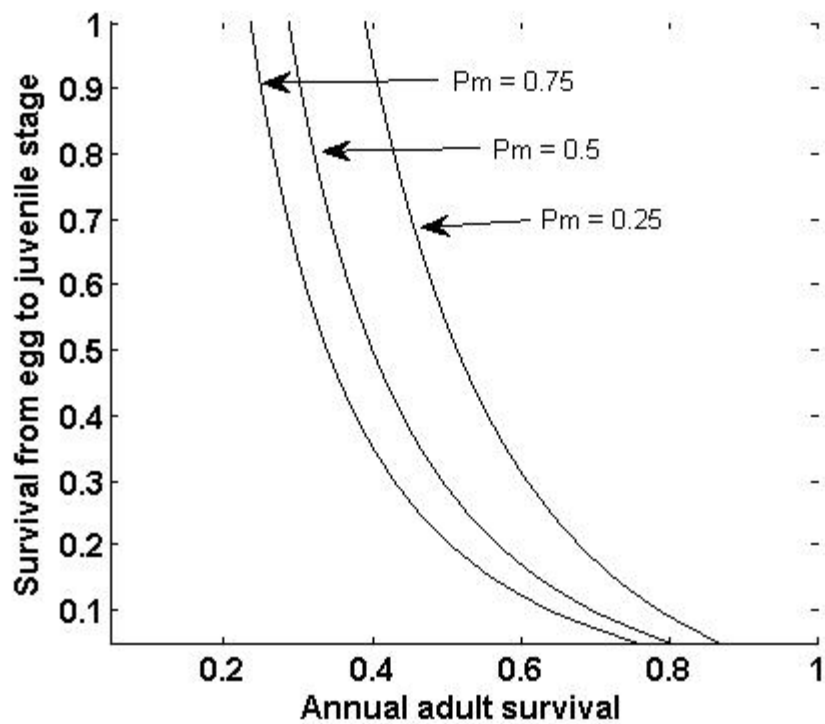
Figure A-28: Output of a deterministic matrix model for an amphibian using parameters given in Table A-4. The three lines represent different models in which the mean annual probability a juvenile becoming reproductively mature (Pm) is 75%, 50% and 25%, mean egg survival is 75%, and mean annual probability of breeding (Pb) is 40%.
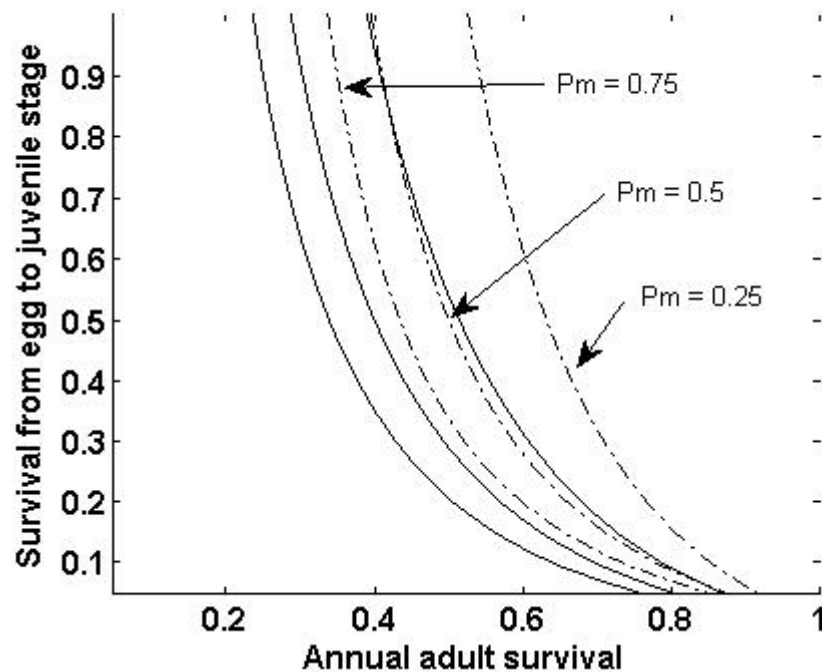
Figure A-29: Output of a stochastic matrix model (dashed lines) for an amphibian using parameters given in Table A-4, with the annual probability a juvenile becoming reproductively mature (Pm) varying at 75% of its maximum σ, and all other parameters vary at 25% of their maximum σ values. The three lines represent different models in which the mean annual probability a juvenile becoming reproductively mature (Pm) is 75%, 50% and 25%, mean egg survival is 75%, and mean annual probability of breeding (Pb) is 40%. Solid lines are results from the deterministic model (as in Figure A-28).
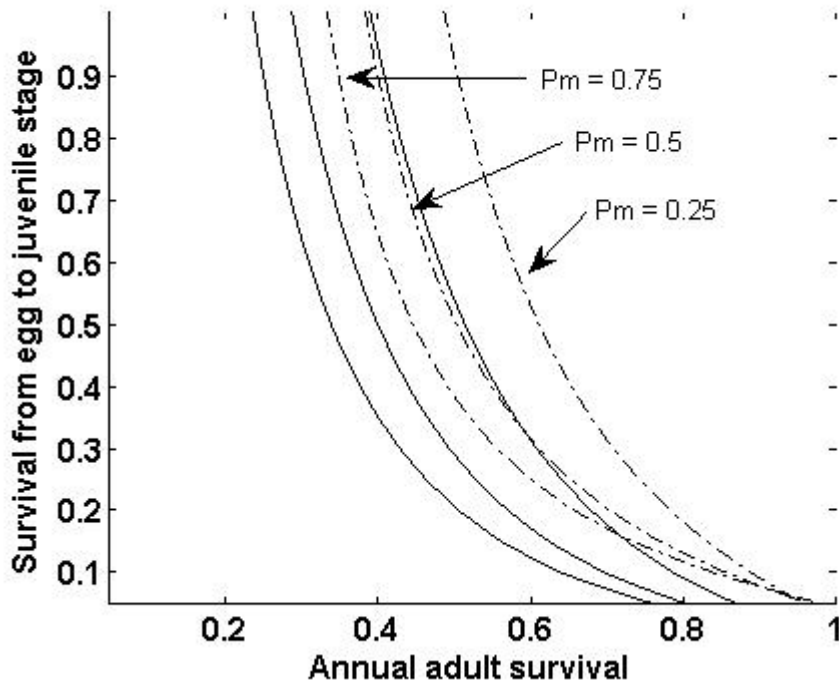
Figure A-30: Output of a stochastic matrix model (dashed lines) for an amphibian using parameters as given in Table A-4, with the probability of survival from the egg to juvenile stage (S_0) varying at 75% of its maximum σ, and all other parameters vary at 25% of their maximum σ values. The three lines represent different models in which the mean annual probability a juvenile becoming reproductively mature (Pm) is 75%, 50% and 25%, mean egg survival is 75%, and mean annual probability of breeding (Pb) is 40%. Solid lines are results from the deterministic model (as in Figure A-28).
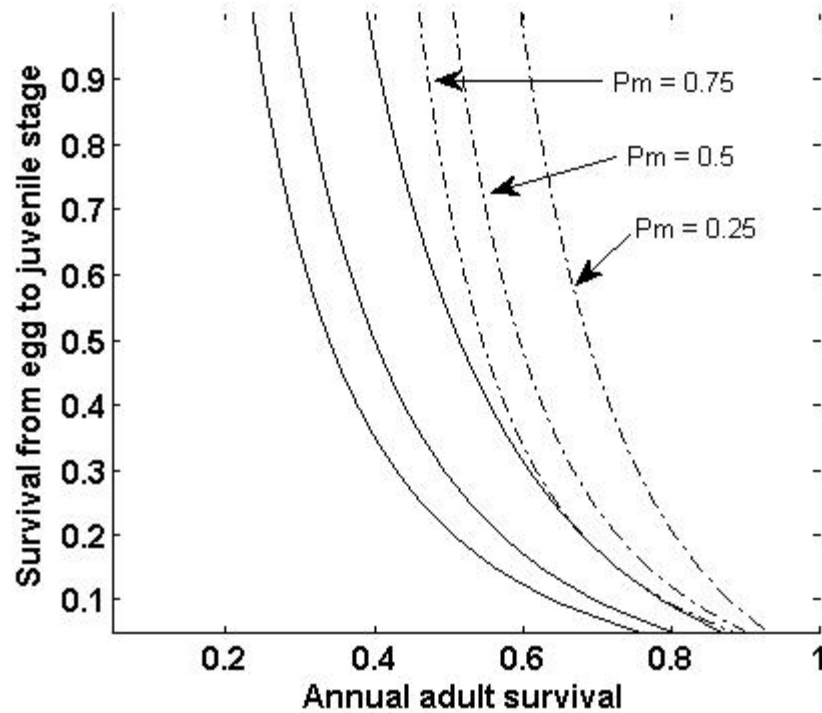
Figure A-31: Output of a stochastic matrix model (dashed lines) for an amphibian using parameters given in Table A-4, with annual adult and juvenile survival (Sa, Sj) varying at 75% of their maximum σ, and all other parameters vary at 25% of their maximum σ values. The three lines represent different models in which the mean annual probability a juvenile becoming reproductively mature (Pm) is 75%, 50% and 25%, mean egg survival is 75%, and mean annual probability of breeding (Pb) is 40%. Solid lines are results from the deterministic model (as in Figure A-28).

5) A general model for birds maturing at 1 year of age
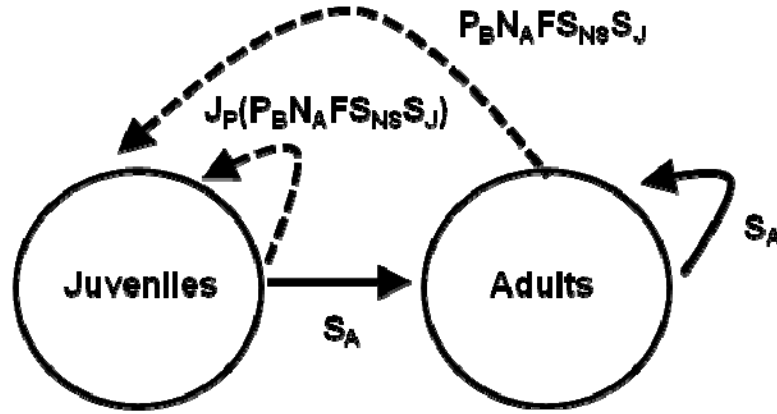
Figure A-32: A general life cycle of a bird maturing at 1 year of age.

$$\begin{bmatrix} J_p\left(0.5\left(N_A\,P_B F S_{NS} S_J\right)\right) & 0.5\left(N_A\,P_B F S_{NS} S_J\right) \\ S_A & S_A \end{bmatrix}$$

Figure A-33: A general model for a bird maturing at 1 year of age.

Table A-5: Parameter definitions and values used for the model of a bird maturing at one year of age. Parameters values based on the Grasshopper sparrow.

Parameter	Values used	Definition	Values in literature
S_{NS}	0.05 – 1.0	nest success	< 0.25 to 0.5[b]
N_A	2, 3	number of nesting attempts per year	1- 4[b]
S_J	0.15, 0.3, 0.75	survival from fledging to first spring	0.35[a]
S_A	0.05 – 1.0	annual adult survival	0.51[a]
P_B	0.9	proportion breeding	
F	3.65	mean clutch size	3.25 – 4.17[b]
J_P	1.0, 0.5	Scaling factor for 1st year breeders reproductive output	
(sex ratio)	0.5	sex ratio is 1:1	

[a]Perkins et al. 2008. [b]Vickery, 1996.
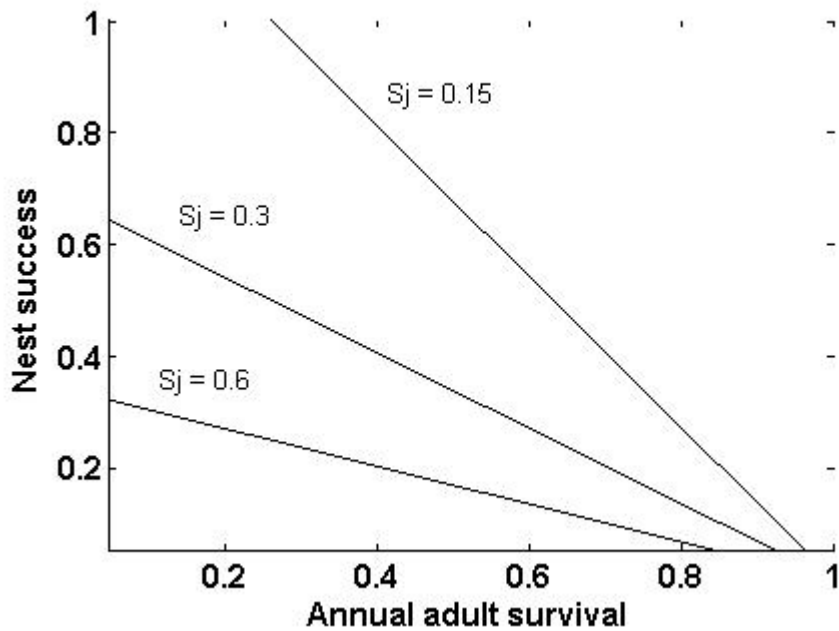
Figure A-34: Results from a deterministic stage-structured model of a Florida grasshopper sparrow (Table A-5), with juvenile reproductive output equal to that of adults. In a stage-structured model, high annual adult survival results in extremely long-lived individuals, and the population does not decline even with nest success as low as 5%.
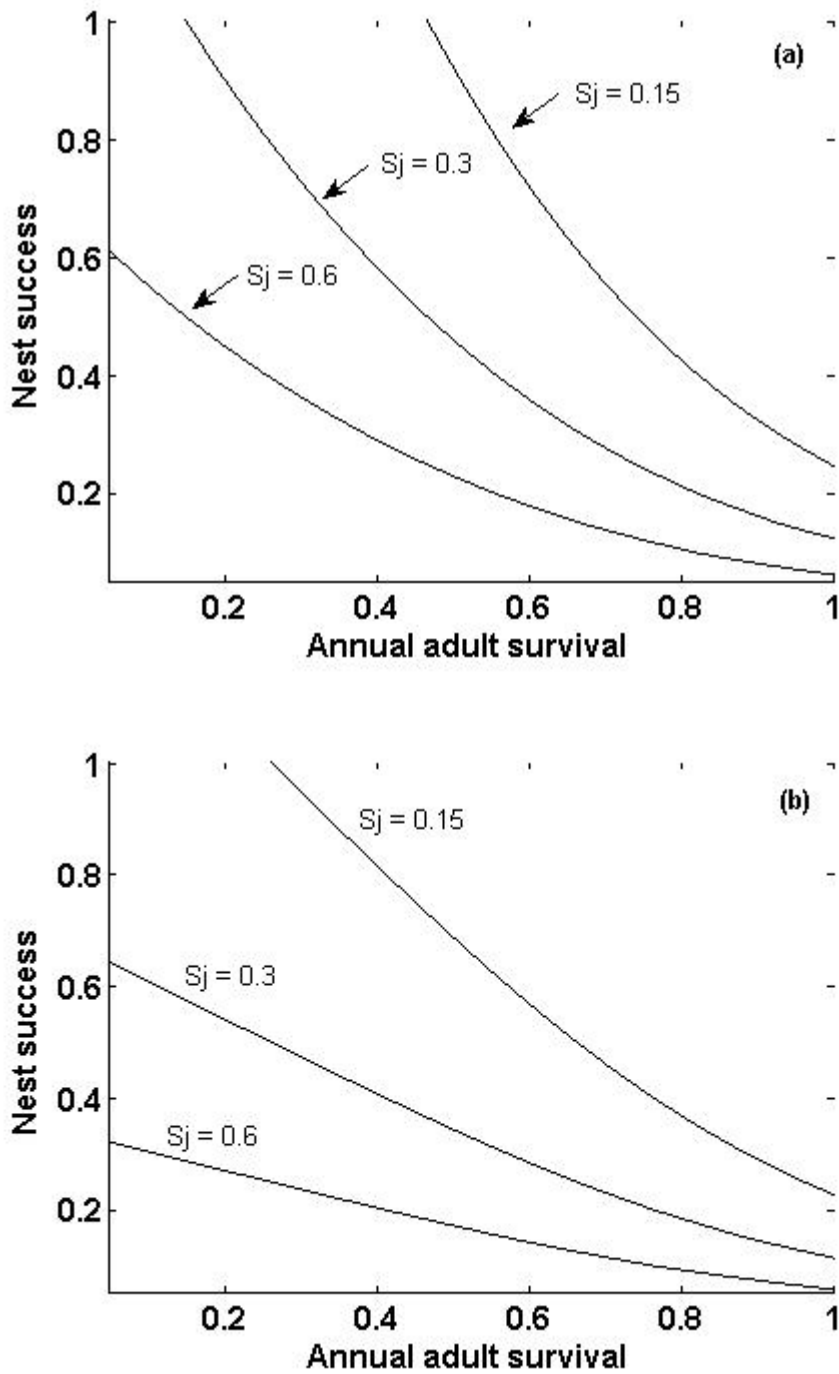
Figure A-35: Output of an age-structured deterministic matrix model for a passerine that breeds in its first year of life (based on data from the Grasshopper sparrow, Table A-5) when (a) juvenile reproductive output is half that of an adult; and (b) equal to that of an adult.
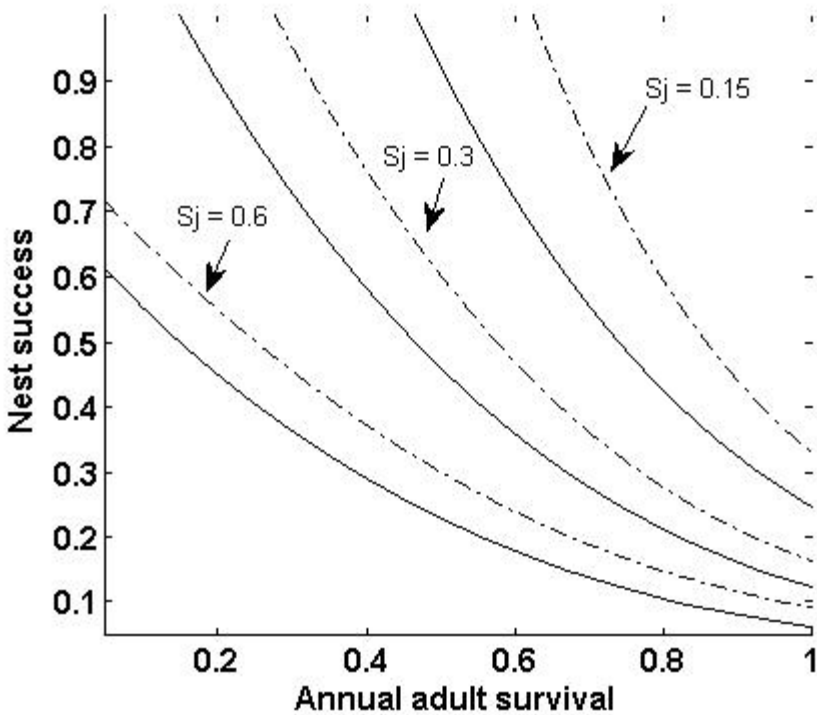
Figure A-36: Output of a stochastic age-structured matrix model (dashed lines) for the Florida Grasshopper sparrow (parameter values given in Table A-5), with all parameters vary at 25% of their maximum σ values. The three lines represent different models in which the mean annual survival of juvenile birds (Sj) is 60%, 30% and 15%, and juvenile reproductive output is always half that of adults. Solid lines are results from the deterministic model (as in Figure A-35a).
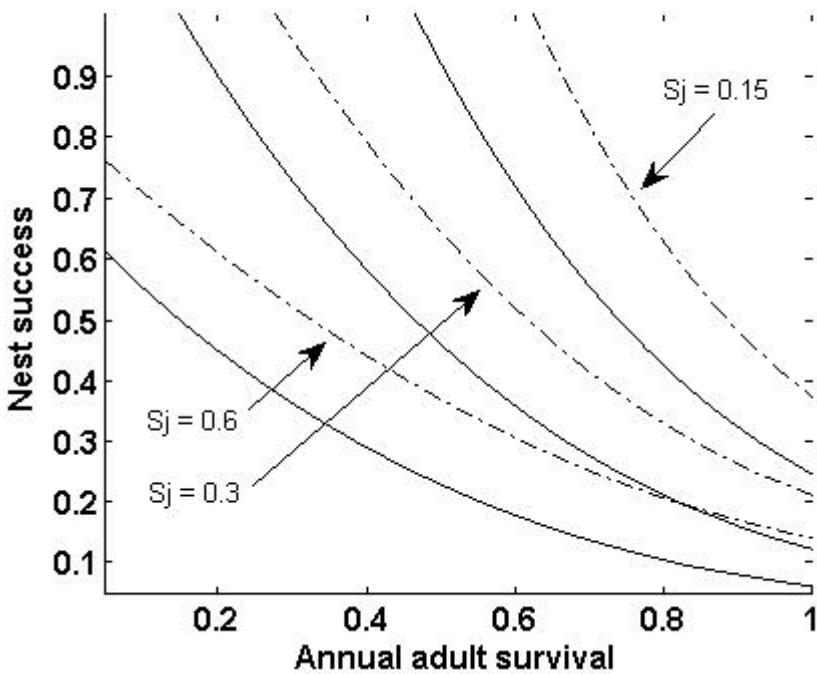
Figure A-37: Output of a stochastic age-structured matrix model (dashed lines) for the Florida Grasshopper sparrow (parameter values given in Table A-5). Nest success varies at 75% of its maximum σ value while all other parameters vary at 25% of their maximum σ values. The three lines represent different models in which the mean annual survival of juvenile birds (Sj) is 60%, 30% and 15%, and juvenile reproductive output is always half that of adults. Solid lines are results from the deterministic model (as in Figure A-35a).
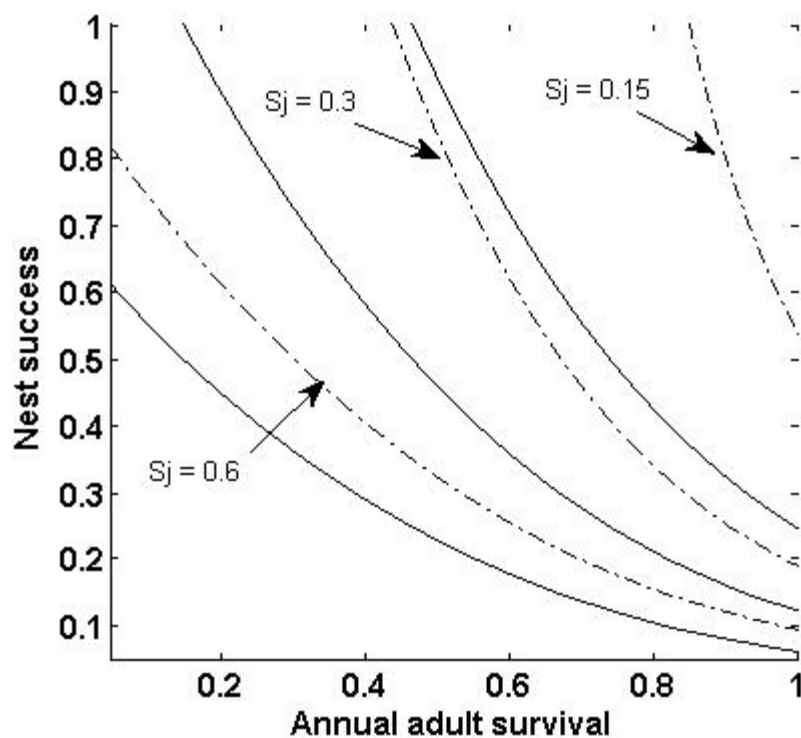
Figure A-38: Output of a stochastic age-structured matrix model (dashed lines) for the Florida Grasshopper sparrow (parameter values given in Table A-5). Juvenile survival varies at 75% of its maximum σ value while all other parameters vary at 25% of their maximum σ values. The three lines represent different models in which the mean annual survival of juvenile birds (Sj) is 60%, 30% and 15%, and juvenile reproductive output is always half that of adults. Solid lines are results from the deterministic model (as in Figure A-35a).
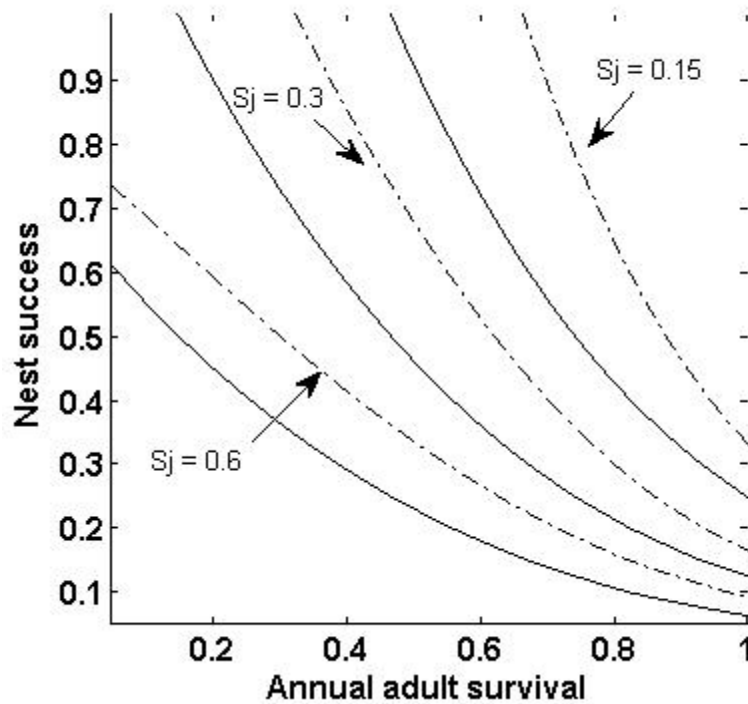
Figure A-39: Output of a stochastic age-structured matrix model (dashed lines) for the Florida Grasshopper sparrow (parameter values given in Table A-5). Adult survival varies at 75% of its maximum σ value while all other parameters vary at 25% of their maximum σ values. The three lines represent different models in which the mean annual survival of juvenile birds (Sj) is 60%, 30% and 15%, and juvenile reproductive output is always half that of adults. Solid lines are results from the deterministic model (as in Figure A-35a).

6) A model for a long-lived, slow maturing bird (Dark-rumped petrel)
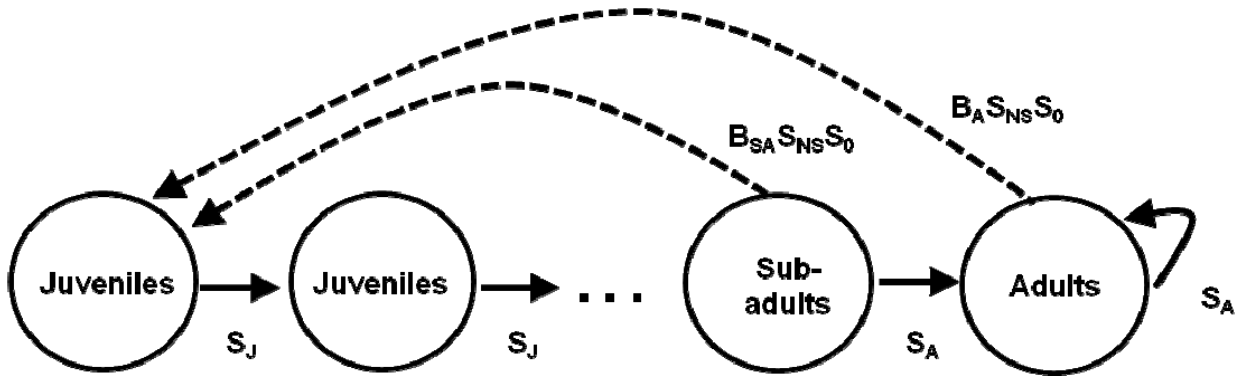
Figure A-40: Dark-rumped petrel life cycle.

$$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 & (\mathbf{B_{SA}S_{NS}S_0})0.5 & (\mathbf{B_A S_{NS} S_0})0.5 \\ \mathbf{S_J} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \mathbf{S_J} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \mathbf{S_J} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \mathbf{S_J} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \mathbf{S_J} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \mathbf{S_J} & \mathbf{S_A} \end{bmatrix}$$

Figure A-41: Model for Dark-rumped petrel.

Table A-6: Parameter definitions and values used for the dark-rumped petrel model (a long-lived, slow maturing bird).

Parameter	Range used	Values in literature	Definition
S_{NS}	0.05 – 1.0	0.35 – 0.72[a]	nest success
S_0	0.05 – 1.0		survival from fledging to 1 year old
S_J	0.7 – 0.9	0.8 [a]	annual survival of juvenile
S_A	0.75 – 0.95	0.8 – 0.93 [a]	annual adult survival
B_{SA}	0.89	0.89 [a]	probability sub-adult breeds
B_A	0.89	0.89 [a]	probability adult breeds
(maturation age)	6 years old	6 years old[a]	age at reproductive maturity
(sex ratio)	1:1		sex ratio

[a] Simons, 1984

Model Output
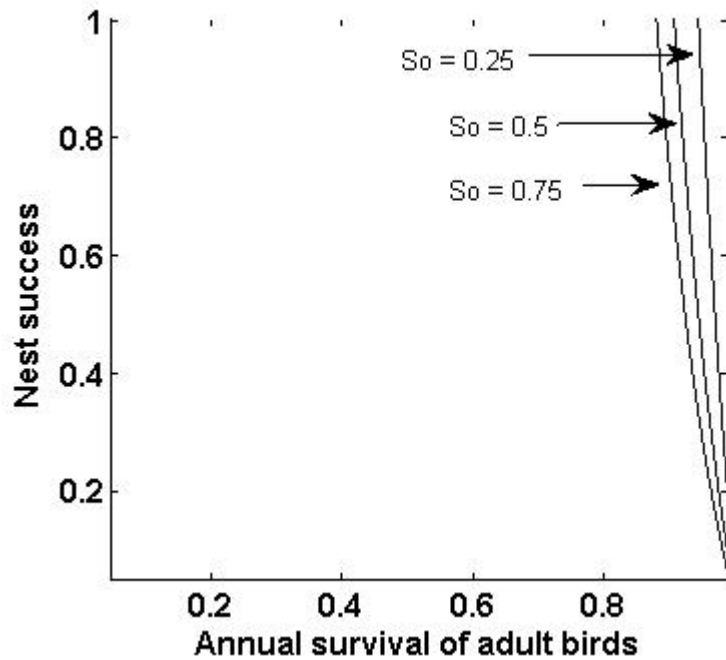
Figure A-42: Comparing the effect of nest success and annual adult survival on the output of an age-structured deterministic matrix model for a long-lived, slow to mature bird (based on data from the Dark-rumped petrel, Table A-6). The different lines represent model output for different values of mean survival from fledging to one year old (S_0 of 75%, 50% and 25%).
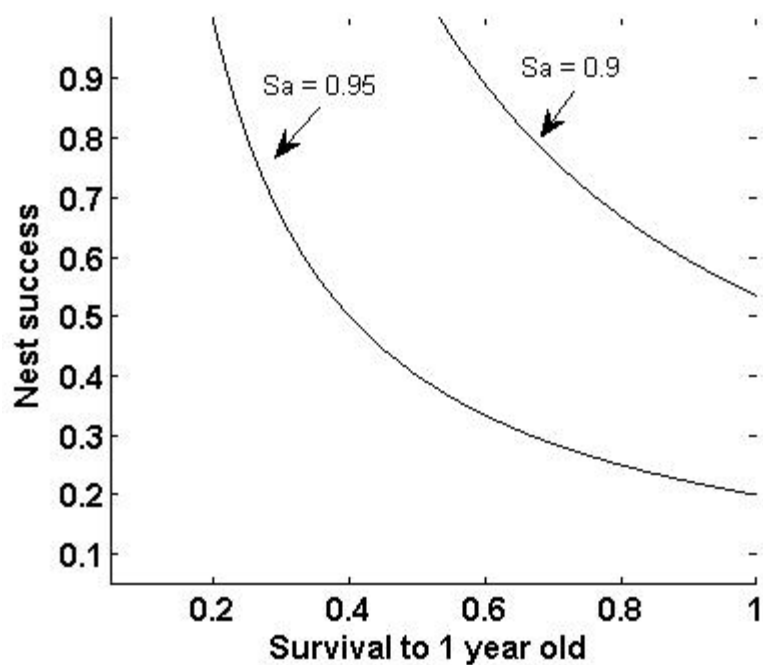
Figure A-43: Comparing the effect of nest success and survival from fledging to 1 year of age on the output of an age-structured deterministic matrix model for a long-lived, slow to mature bird (based on data from the Dark-rumped petrel, Table A-6). The lines represent model output for changing values of mean annual adult survival (Sa) of 95% and 90%.
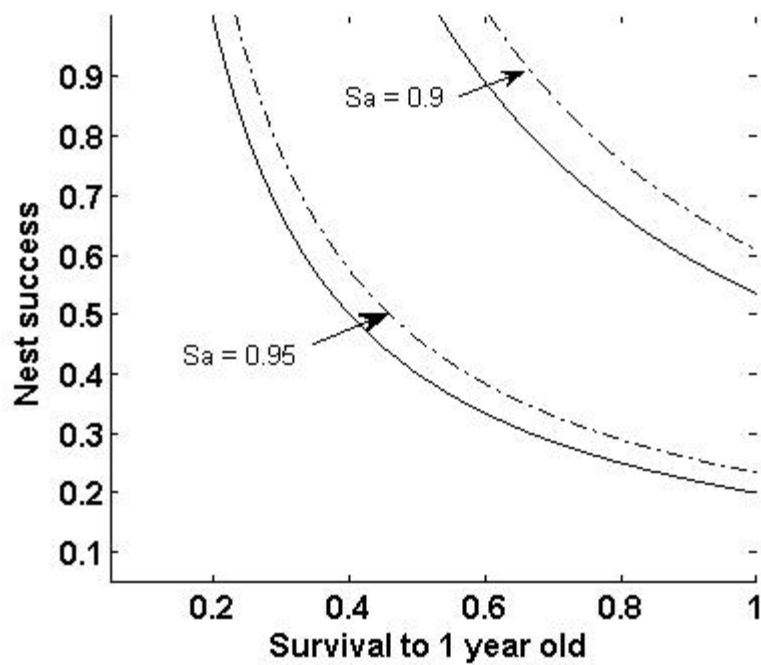
Figure A-44: Output of a stochastic age-structured matrix model (dashed lines) for the Dark-rumped petrel (Table A-6). Nest success and survival from fledging to 1 year of age vary at 75% of their maximum σ values while all other parameters vary at 25% of their maximum σ values. The two lines represent different models in which the mean annual survival of adult birds (Sa) is 95% and 90%. Solid lines are results from the deterministic model (as in Figure A-43).
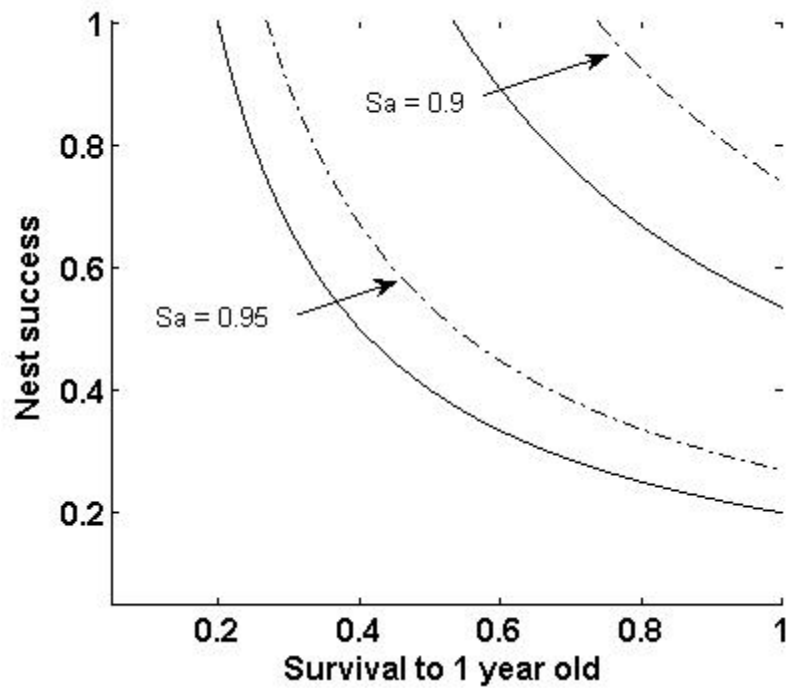
Figure A-45: Output of a stochastic age-structured matrix model (dashed lines) for the Dark-rumped petrel (Table A-6). Annual adult and juvenile survival vary at 75% of their maximum σ values while all other parameters vary at 25% of their maximum σ values. The two lines represent different models in which the mean annual survival of adult birds (Sa) is 95% and 90%. Solid lines are results from the deterministic model (as in Figure A-43).

7) A model for a long-lived, slow maturing turtle (the bog turtle)
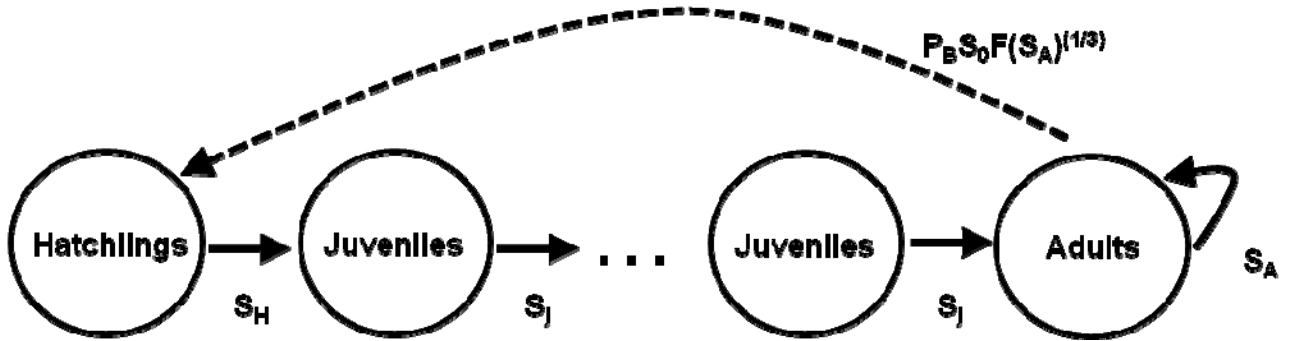
Figure A-46: Life cycle for the bog turtle.

$$
\begin{bmatrix}
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \left((S_A)^{1/3} P_B F S_0 \right) 0.5 \\
S_H & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & S_J & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & S_J & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & S_J & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & S_J & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & S_J & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & S_J & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & S_J & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_A
\end{bmatrix}
$$

Figure A-47: Model for bog turtle.

Table A-7: Parameter definitions and values used for the bog turtle model.

Parameter	Values used	Values in literature	Definition
S_0	0.1 - 1.0	0 - 0.74[a] 0.47 - 0.411[e]	survival from egg to hatchling emergence from nest
S_H	0.3 - 0.7		hatchling survival (1st year above ground)
S_J	0.5(S_A); 0.75(S_A); 1.0(S_A)	0.753 - 0.921[e]	annual juvenile survival
S_A	0.1 - 1.0	0.932[b] 0.775 - 0.957[e]	annual adult survival
P_B	0.7 - 0.9[d]	0.7 - 0.9[d]	proportion breeding
F	3	1 - 5[c]	mean clutch size
(maturation age)	10 years old[c]		age at reproductive maturity
(sex ratio)	0.5		sex ratio 1:1

[a]Carroll and Ultsch, 2007; [b]Converse et al 2005; [c]USFWS, 2001; [d]Griffen, 2007; [e]Iverson, 1991
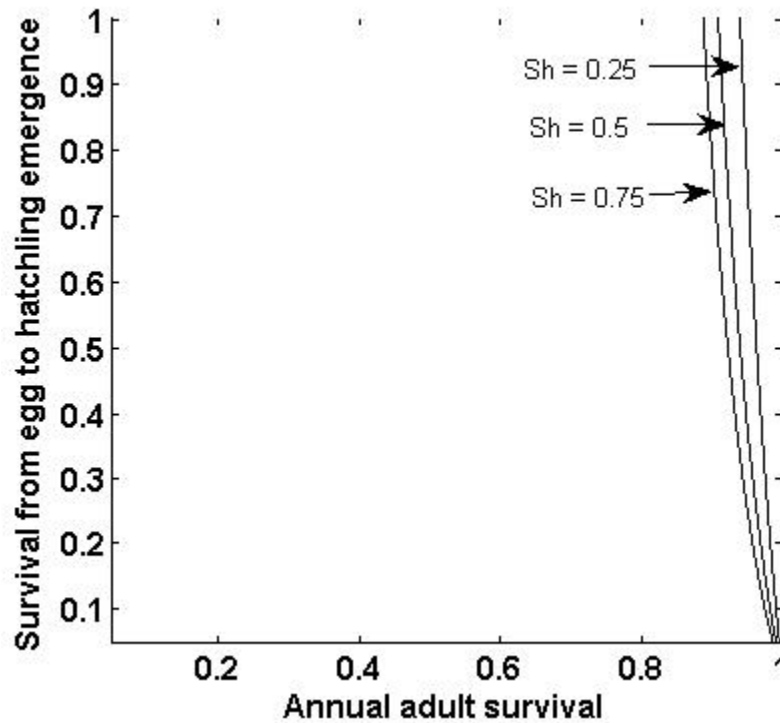
Figure A-48: Comparing the effect of annual adult survival and survival from egg to hatchling emergence on the output of an age-structured deterministic matrix model for a long-lived, slow to mature turtle (based on data from the Bog turtle, Table A-7). The lines represent model output for changing values of mean hatchling survival (Sh) of 75%, 50% and 25%.
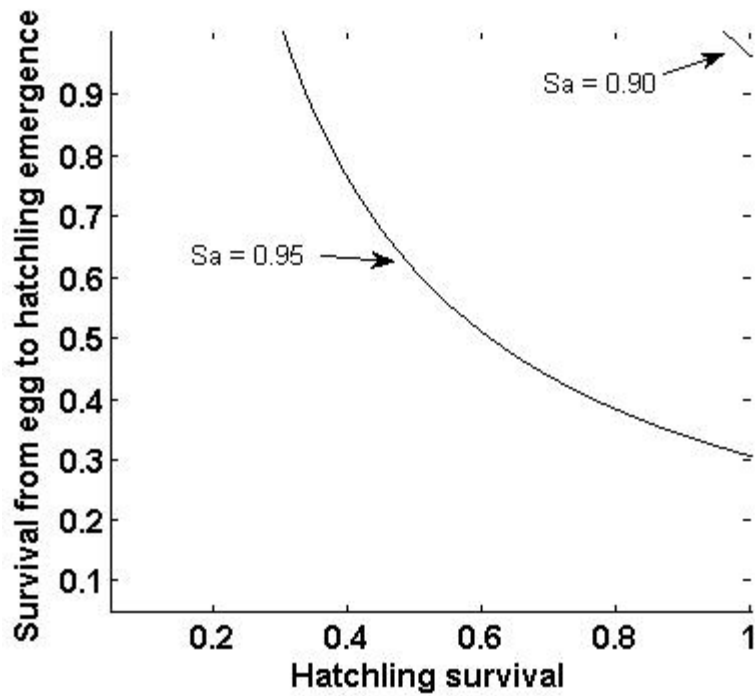
Figure A-49: Comparing the effect of hatchling survival and survival from egg to hatchling emergence on the output of an age-structured deterministic matrix model for a long-lived, slow to mature turtle (based on data from the Bog turtle, Table A-7). The lines represent model output for changing values of mean annual adult survival (Sa) of 95% and 90% and mean annual juvenile survival is 0.8*Sa.
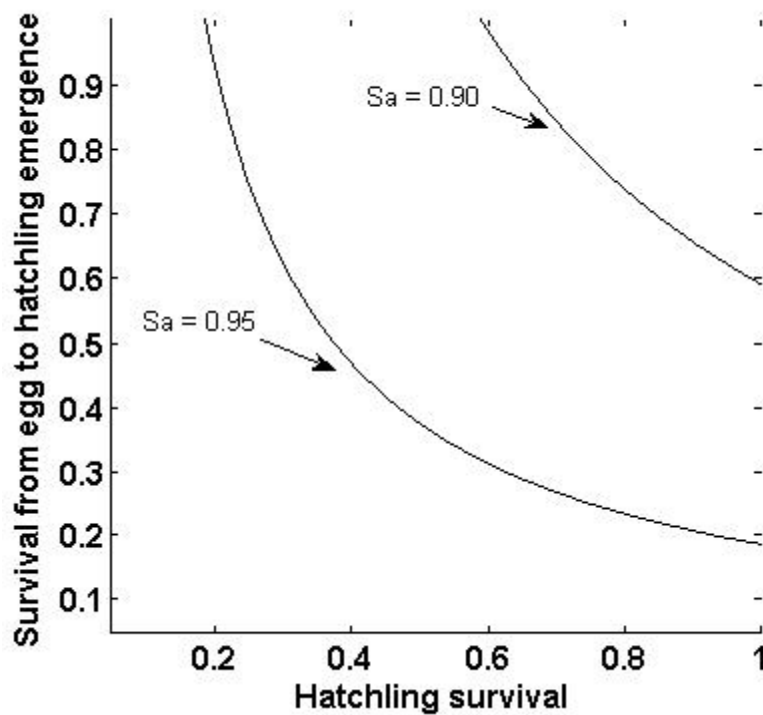
Figure A-50: Comparing the effect of hatchling survival and survival from egg to hatchling emergence on the output of an age-structured deterministic matrix model for a long-lived, slow to mature turtle (based on data from the Bog turtle, Table A-7). The lines represent model output for changing values of mean annual adult survival (Sa) of 95% and 90% and mean annual juvenile survival is 0.85*Sa.
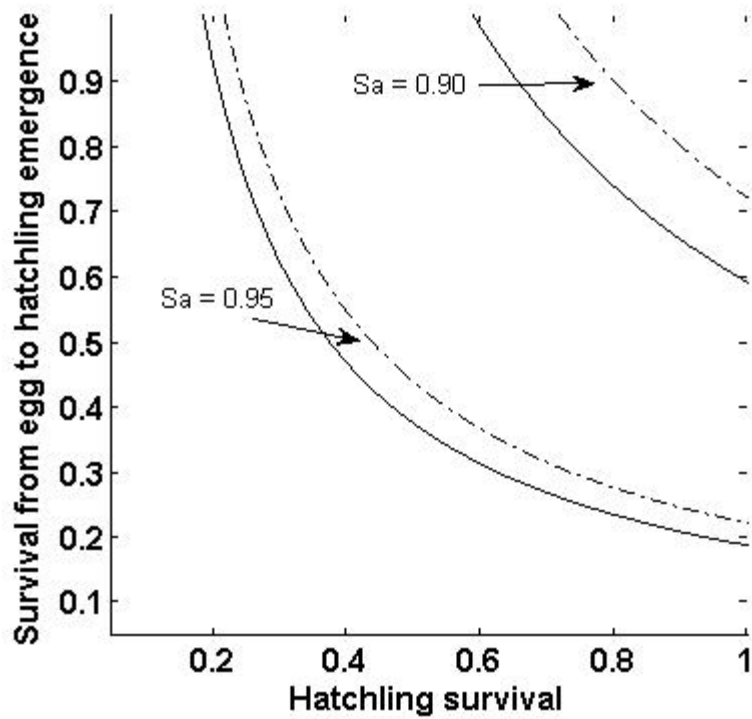
Figure A-51: Output of a stochastic age-structured matrix model (dashed lines) for a long-lived, slow to mature turtle (based on data from the Bog turtle, Table A-7), in which all parameters vary at 25% of their maximum σ values. The lines represent model output for changing values of mean annual adult survival (Sa) of 95% and 90%. Solid lines are results from the deterministic model (as in Figure A-50).
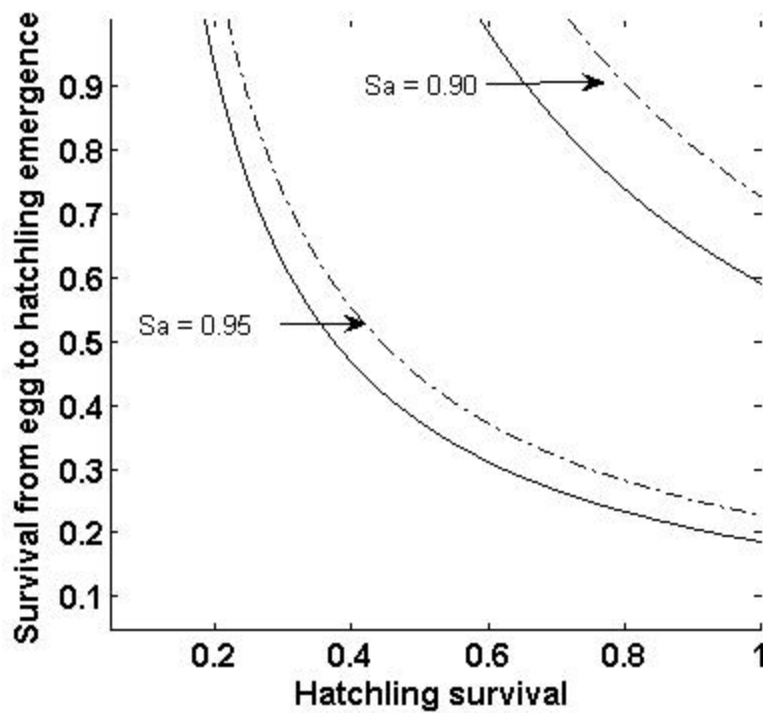
Figure A-52: Output of a stochastic age-structured matrix model (dashed lines) for a long-lived, slow to mature turtle (based on data from the Bog turtle, Table A-7). Hatchling survival (S0) and survival from egg to hatchling emergence (Sh) vary at 75% of their maximum σ values while all other parameters vary at 25% of their maximum σ values. The lines represent model output for changing values of mean annual adult survival (Sa) of 95% and 90% and mean annual juvenile survival is 0.85*Sa. Solid lines are results from the deterministic model (as in Figure A-50).
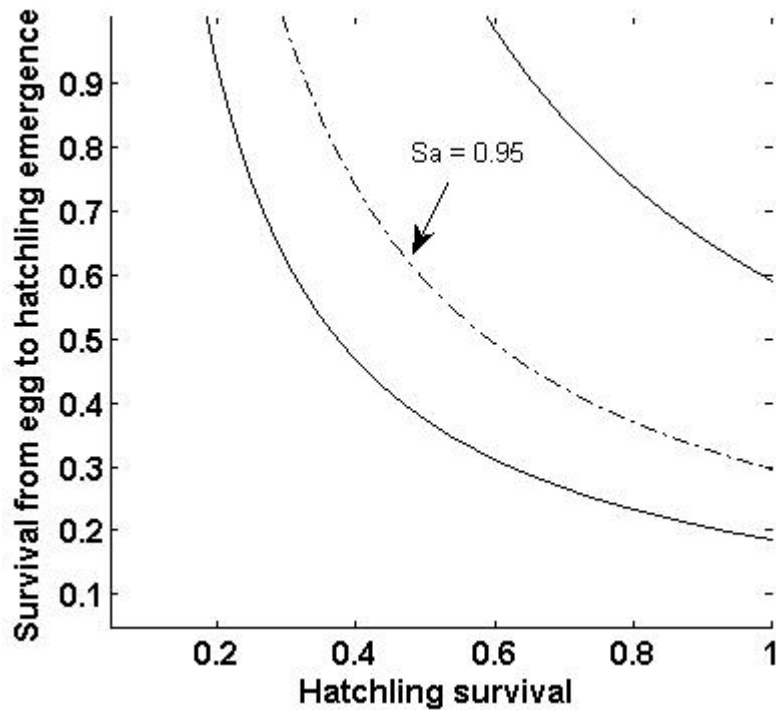
Figure A-53: Output of a stochastic age-structured matrix model (dashed lines) for a long-lived, slow to mature turtle (based on data from the Bog turtle, Table A-7). Annual adult (Sa) and juvenile survival (Sj) vary at 75% of their maximum σ values while all other parameters vary at 25% of their maximum σ values. The lines represent model output for changing values of mean annual adult survival (Sa) of 95% and 90% and mean annual juvenile survival is 0.85*Sa. Solid lines are results from the deterministic model (as in Figure A-50).

8) **A general model for small mammals**
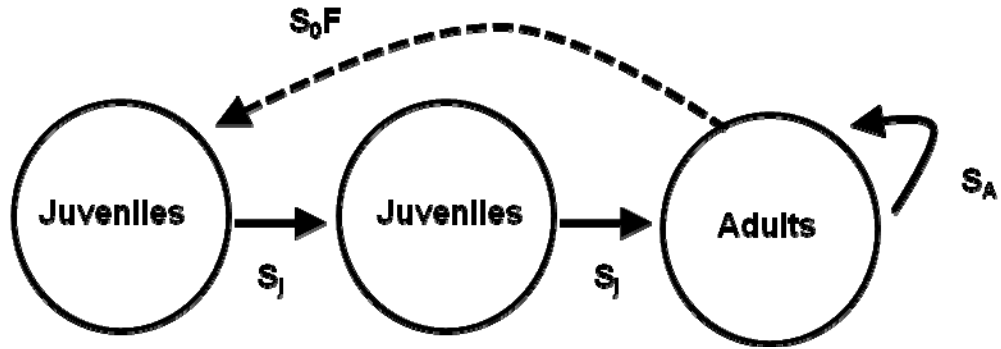
Figure A-54: General life cycle for a small mammal.

$$A_B = \begin{bmatrix} 0 & 0 & 0.5(S_0F) \\ S_J & 0 & 0 \\ 0 & S_J & S_A \end{bmatrix} \qquad A_{NB} = \begin{bmatrix} 0 & 0 & 0 \\ S_J & 0 & 0 \\ 0 & S_J & S_A \end{bmatrix}$$

A_B = monthly matrix (breeding season)
A_{NB} = monthly matrix (non-breeding season)

Yearly matrix $A = (A_{NB})^3(A_B)^9$

Figure A-55: General model for a small mammal.

Table A-8: Parameter definitions and values used for the model of a small mammal, with parameters values used in the model based on Stephen's kangaroo rat.

Parameter	Values used	Definition	Values in literature
S_0	0.25, 0.5, 0.75	survival of 0-1 month old pups	0.25[a], 0.39[a], 0.43[b]
S_J	$(0.5*S_A)$, $(0.8*S_A)$	monthly survival of juveniles	0.35[a]
$S_{A(NB)}$	0.05 – 1.0	monthly adult survival in non-breeding season	0.18 – 0.59[a]
$S_{A(B)}$	0.05 – 1.0	monthly adult survival in breeding season	0.18 – 0.59[a]
F	2	mean litter size	1.5 – 2.67[a,c]
(sex ratio)	0.5	sex ratio is 1:1	
(breeding season)	9 months	breeding season	"rainy season"[a]

[a] Price and Kelly, 1994; [b]Lackey, 1967; [c] Randall, 1991

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Appendix B. Scientific Publications

Scientific Publications

Humbert, Jean-Yves, L. Scott Mills, Jon S. Horne and Brian Dennis. 2009. A better way to estimate population trends. Oikos 118:1940-1946.

Dennis, Brian, José Miguel Ponciano, and Mark L. Taper. *In press*. Replicated sampling increases efficiency in monitoring biological populations. Ecology.

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Neel, Maile C., Allison K. Leidner, Aaron Haines, Dale D. Goble, and J. Michael Scott. *In review.* By the numbers: how is recovery defined by the U.S. Endangered Species Act?

Hartway, C. R. and L. S. Mills. *In review.* A meta-analysis assessing management impacts on avian nest success. Conservation Biology.

Horne, Jon S., Katherine M. Strickler, and Mathew Alldredge. *In press.* Quantifying the importance of patch-specific changes in habitat to metapopulation viability of an endangered songbird. Ecological Applications.

Workshops at National Professional Conferences

1. The Wildlife Society Annual Conference, Miami, FL, November 2008

On November 8, 2008 Drs. E. O. Garton, J. S. Horne, and L. S. Mills presented a workshop, "Using Sensitivity Analysis of Population Viability Models to Guide Management Decisions," at The Wildlife Society Annual Conference in Miami, Florida. The objectives of the workshop were to: (1) review how population viability models (analysis) can be used to inform conservation and management decisions and (2) describe recent developments in PVA that allow prioritization of research and management under widely varying levels of empirical knowledge of the species of interest. When very little is known about the focal species, we introduced a new approach that leverages information from similar, well-studied species to initiate and inform an adaptive management program for the focal species. For species that have been monitored for several years producing time-series of abundance data, we described several stochastic growth models that can be fit to these data and when coupled with environmental covariates, can be used to predict population dynamics under different management scenarios. Finally, when a great deal of empirical data exists to parameterize a matrix-based projection model (single population and metapopulation), we discussed several approaches to sensitivity analysis of these models. Depending on research objectives, results from a rigorous sensitivity analysis can be used to both prioritize future research and evaluate the effect of different management actions on species viability.

This workshop was attended by 21 natural resource managers and research professionals who were interested in learning these new approaches. Attendees were exposed to recently developed web-sites and software that will aid implementation of the approaches. Each participant received a ~50-page binder detailing all material presented and a CD containing copies of new software authored by the organizers as well as pdfs of relevant papers. Workshop materials are included in electronic Appendix C.

2. National Military Fish and Wildlife Association, Washington, DC, March 2009

We hosted a technical session and workshop at the National Military Fish and Wildlife Association meeting in Washington, D.C. on 20 March 2009. The format was a joint technical session providing an overview of a variety of conservation and management tools developed under SERDP funding. The session included individual presentations about the three approaches developed under our project as well as the Effective Area Model developed by Drs. Leslie Ries and Tom Sisk (SI-1597), and the HEXSIM software developed by Drs. Betsy Bancroft, Josh Lawler, and others (SI-1541). Following the session, we offered a two-hour workshop for attendees interested in learning to use the web-sites and software introduced in the technical session. About 20 people participated and we are talking with NMFWA leadership about organizing a similar session at a future meeting.

3. The Wildlife Society Annual Conference, Monterey, CA, September 2009

With Mr. Chris Eberly, director of DoD Partners in Flight, we coordinated a symposium at the annual conference of The Wildlife Society addressing the topic "Conservation-Reliant Species: Our New Relationship with Nature."   Nine presentations by endangered species experts included:

>   Conservation reliant species in a time of change. Michael J. Scott
>
>   Rethinking recovery under the Endangered Species Act in a conservation-reliant world. Dale D. Goble
>
>   Conservation-reliant big game: The critical aspects of management. Paul Krausman
>
>   Managing the Mission and Endangered Species at Marine Corps Base Camp Pendleton. Beth Forbus, William H. Berry, Eric Kershner
>
>   Conservation-reliant birds of Hawaii: Alien species, disease, and climate change. J. Michael Reed, David W. DesRochers, Eric VanderWerf, J. Michael Scott
>
>   Conservation of the California Condor: Are self-sustaining populations possible. Jesse Grantham, Jeffrey R. Walters, Matthew Johnson
>
>   How does a completely conservation-reliant species ever recover under the Endangered Species Act? Lessons from the Kirtland's Warbler. Carol Bocetti
>
>   Are some game species conservation reliant species? Edward O. Garton
>
>   Application of post-recovery management principles to maintenance of species at risk. Erica Fleishman

The recovery and delisting of threatened or endangered species has traditionally been achieved when species-specific management is no longer necessary. However, the magnitude and pace of human impacts on the environment may require a definition of recovery that includes some form of species-specific post-recovery management. Many listed species rely on management intervention for which a threat cannot be eliminated, only controlled. Recovery of these conservation-reliant species can be achieved in numbers and distributions consistent with recovery goals, but will require a new model of recovery planning. This symposium will present the concept of conservation-reliant species and will explore a number of species along the conservation reliance continuum. The Symposium will also look at the factors that influence the species and their potential for recovery.

4. SERDP-ESTCP Partners in Environmental Technology Technical Symposium, December 2008

Dr. J. Michael Scott and Dr. John Hall coordinated a technical session at the 2008 SERDP-ESTCP Partners in Environmental Technology Technical Symposium. Titled "Science Underlying the Post-Recovery Management of Listed Species," the session was chaired by Dr. Deborah Crouse of the U.S. Fish and Wildlife Service, with Dr. Scott delivering the keynote address. The overall topic of the session was the underlying science issues involved with the post-recovery management of listed species, from those that require little continued intervention to maintain their populations to those that might require long-term management attention. Individual presentations included:

Introduction and Wrap-up: Dr. Deborah Crouse, U.S. Fish and Wildlife Service / Division of Endangered Species

Keynote: Humanity's New Relationship with Nature: Conservation-Reliant Species, Dr. J. Michael Scott, U.S. Geological Survey / University of Idaho

How to Achieve Post-Recovery Habitat Management for a Completely Conservation-Reliant Species: A New Paradigm for the Kirtland's Warbler. Dr. Carol Bocetti, California University of Pennsylvania / Department of Biological and Environmental Sciences

Case Study of the Karner Blue Butterfly: An Example of the Importance of Host Species Management in Post-Recovery Management. Dr. Ralph Grundel, U.S. Geological Survey / Great Lakes Science Center, Lake Michigan Ecological Research Station

Carrying Conservation Forward: Post-Recovery Management and Monitoring for Eggert's Sunflower (*Helianthus eggertii*). Mr. Geoff Call, U.S. Fish and Wildlife Service / Cookeville Field Office

Aleutian Cackling Goose Recovery: From the Brink of Extinction to Becoming Just Another Migratory Goose. Mr. Vernon Byrd, U.S. Fish and Wildlife Service / Alaska Maritime National Wildlife Refuge

Application of Science Principles for Post-Recovery Management of Listed Species to At-Risk Species. Dr. Erica Fleishman, University of California, Santa Barbara / National Center for Ecological Analysis and Synthesis

Site-Specific Conferences

Yakima Training Center, Yakima, Washington, March 2009

On 26 March 2009 Drs. Oz Garton, Jon Horne, Katherine Strickler, J. Michael Scott, and Brian Dennis presented a workshop, "Tools for Assessing Population Trend and Viability in Greater Sage-grouse," at Yakima Valley Community College in Yakima, Washington. The objectives of the workshop are to: 1) review methods of estimating population trend and sensitivity, 2) introduce software programs developed at University of Idaho to estimate population viability (PopGrowth and MetaPVA), 3) present results of sage-grouse population trend and viability analyses for Yakima Training Center, and 4) obtain feedback from participants regarding software products and analyses. The workshop was attended by seven members of the YTC environmental staff as well as biologists from U.S. Fish and Wildlife Service and the Yakama Nation. Each participant received a ~70-page binder detailing all material presented, a PopGrowth tutorial, and a CD containing copies of the PopGrowth software. It was an informal setting characterized by tremendously productive discussions of important sage-grouse issues facing YTC, FWS, and tribal managers. Sage-grouse are a state-listed species in Washington and their continuing decline has high potential to constrain training at YTC. After learning more about the software and reviewing our results, YTC environmental staff identified additional management concerns they would like help with and expressed interest in continuing to work with our team to quantify the effects of training and recovery activities on sage-grouse at YTC and in Washington as a whole. Workshop materials are included in electronic Appendix C.

1.   NATIONAL MILITARY FISH AND WILDLIFE ASSOCIATION, PORTLAND, OR, MARCH 2007

     TITLE: NEW TOOLS FOR ASSESSING THE EFFECTS OF TRAINING AND MANAGEMENT ON LISTED SPECIES ON DEPARTMENT OF DEFENSE LANDS

AUTHORS: J. Michael Scott, USGS; L. Scott Mills (presenting author), University of Montana; E.O Garton, University of Idaho; Matthew Kauffman, University of Wyoming; Cynthia Hartway, University of Montana; Jon Horne, University of Idaho; Katherine Strickler, University of Idaho

ABSTRACT: Military managers are increasingly faced with challenges of balancing endangered species conservation with military missions and the need for training readiness. While military agencies do not establish recovery goals for listed species, training activities must not impede the recovery of listed species that occur on or near training areas. In many cases, military managers are uniquely situated to enhance local populations of endangered species. Department of Defense (DoD) lands cannot recover endangered species alone but they can facilitate more robust populations that will allow more flexible training options. This challenge is often complicated by two related limitations: a) incomplete information about endangered species that precludes conducting quantitative, complex viability analyses to assess the effects of training or conservation activities on populations of listed species on DoD lands; and b) the lack of user-friendly software to prioritize data needs and guide users through a population viability analysis dependent on available biological information as well as potential management activities and training scenarios.

We are developing a scientifically-based system of tools and protocols that will help DoD managers meet population goals for listed species and assess the effects of training options on these species, while continuing to support military missions. A key element of our approach is to develop tools for population recovery that, for a given species, are appropriate to the amount of biological data available.

The overall objective of this program is to provide managers with a set of alternative approaches that can be used to estimate extinction risk or prioritize management actions that simultaneously meet population goals while facilitating goals of military training. Under this approach, resource managers will use existing data on listed species to select the optimum approach for analyzing population responses to management activities and environmental variables. The selected analysis and modeling approach will then be combined with information on important threats to the species, potential management options and their associated costs, and key demographic and topographic parameters to

project population consequences of selected management options. These projections will provide a sound basis for managers to consult with USFWS and NOAA Fisheries to implement training and management actions and monitor the population response of listed species.

Specifically, the optimum approach for each species will be selected from an array of alternative approaches. For little-known species having insufficient data to parameterize a population viability model, we will provide protocols for management prioritization based on our "Life History Typology" (LHT) analysis. We base the LHT analysis on an extensive database and meta-analysis in which we determine, for well-studied species, the proportional effect each vital rate has on population growth (e.g. elasticity), the amount each vital rate changes in nature (process variance), and the extent to which particular management perturbations can change vital rates (vulnerability). The typologies, or generalizations across taxonomic groups or management actions for these well-studied species, will provide the basis for ranking management actions for endangered species on DoD sites for which data are lacking.

For better-studied species, population viability models can be used to assess the impact of training/management activities on species recovery. However, empirical data used to populate these models can range from a simple time-series of relative abundance to spatially explicit information on metapopulation structure and dynamics. Similarly, models for analyzing population viability range from simple deterministic single population models to stochastic single population models to spatially explicit stochastic metapopulation and individual-based models. Our analysis will a) identify what types of empirical data are critical for estimating species viability and b) determine what level of model complexity is needed in order to determine the effect of site-specific management scenarios on overall species viability. We will also be developing analytical software suitable for use by DoD biologists on individual species assessments for their respective military installations.

We will test the analytical approach and software with empirical data for four listed species that are currently of management concern on DoD lands. We will also use the approach to validate our methods and evaluate the factors most responsible for recovery of several species that have been de-listed or down-listed. Finally, we will work with DoD biologists, managers and other stakeholders to develop and test the LHT approach and spatial analyses using site-specific empirical examples, and present training sessions for DoD biologists at national and regional meetings.

The products of the proposed research will include: 1) a database of life history typologies for species representing a broad range of taxonomic groups, life history characteristics and management sensitivities that will provide information to develop

rules of thumb for the response of species to training activities and proposed management and conservation actions; 2) quantitative predictions as to the influence a single population (i.e., military installation) will have on overall population persistence given a variety of metapopulation structures and dynamics; 3) user-friendly analytical software to assist DoD biologists in assessing the potential impacts of training activities on populations and metapopulations and in meeting population goals for listed species; and 4) training for DoD biologists in the use of the database and analytical software and assistance in making more efficient and biologically defensible decisions regarding the impacts of DoD actions on listed species. The proposed research will assist DoD natural resource and operations managers in focusing conservation and impact mitigation measures so that they have greater ability to decrease constraints on training activities imposed by legal requirements to protect listed species present on bases.

2.   26TH WESTERN AGENCIES SAGE AND COLUMBIAN SHARP-TAILED GROUSE WORKSHOP, MAMMOTH LAKES, CA, JUNE 2008

TITLE: ALLEE AND RICKER EFFECTS ON PERSISTENCE OF GREATER SAGE GROUSE POPULATIONS

AUTHORS: E.O. Garton, University of Idaho; Jon S. Horne, University of Idaho; Katherine M. Strickler, University of Idaho; Ann Moser, Idaho Department of Fish and Game; Brian Dennis, University of Idaho; J.W. Connelly, Idaho Department of Fish and Game; Michael A. Schroeder, Washington Department of Fish and Wildlife; J. Michael Scott, USGS.

ABSTRACT: The Allee effect, or declining per capita growth rates at low population sizes, could negatively impact the persistence of declining populations of Greater Sage Grouse while the Ricker effect, declining per capita growth rates at higher population sizes produces an objective carrying capacity for stable or increasing populations. We estimated the parameters of a discrete time, stochastic growth model incorporating both the Allee and Ricker effects from annual lek counts in the Snake River Plain, Idaho and eastern Washington 1965-2003. These data provide highly significant evidence for both the Allee and Ricker effects in sage grouse populations. The model provides clear criterion for defining a lower threshold for numbers attending leks below which the populations are likely to decline to extinction. Using this threshold and estimated parameters for the stochastic growth model we could evaluate the probability of persistence or extinction of populations and metapopulations of sage grouse throughout their range. Applying the model to populations varying stochastically at the upper end of

the abundance continuum provides a way to evaluate factors influencing carrying capacity of grouse. Sensitivity analysis can be applied to this model and to stage-structured models of sage grouse populations to identify management actions most likely to reverse the long-term declines of the species throughout the west and predict the probable impacts of global climate change.

3.   SOCIETY FOR CONSERVATION BIOLOGY, CHATTANOOGA, TN, JULY 2008

TITLE: ESTIMATING ECOLOGICAL TREND: WHICH MODEL SHOULD I USE?

AUTHORS: Brian Dennis (presenting author), University of Idaho; Jean-Yves Humbert, ART Research Station, Zurich; L. Scott Mills, University of Montana; Jon S. Horne, University of Idaho

ABSTRACT: Regression of log-abundance of a population versus time is often used to estimate the population's trend. It is not widely realized that such regression carries implicit assumptions about how the trend and the variability in the population abundances arise. If the statistical model does not adequately describe the process by which the data are produced, the trend estimate can be seriously in error. Here we describe three models for estimating population trend. The three are different stochastic versions of the exponential growth model: (1) observation error only, (2) environmental process noise only, and (3) a state space model which combines both observation error and process noise. We describe the statistical methods for obtaining parameter estimates, including estimates of trend, for time series abundance data under each of the three models. Logabundance regression turns out to correspond to deterministic exponential growth with observation error only, that is, model (1).

4.   SOCIETY FOR CONSERVATION BIOLOGY, CHATTANOOGA, TN, JULY 2008

TITLE: IS MY POPULATION RECOVERING, DECREASING, OR STATIONARY? IMPROVING THE STATUS QUO FOR ESTIMATING EXPONENTIAL TREND FROM COUNT DATA

AUTHORS: L. Scott Mills (presenting author), University of Montana; Jean-Yves Humbert, ART Research Station, Zurich; Jon S Horne, University of Idaho; Brian Dennis, University of Idaho

ABSTRACT: An estimate of the trend, or population growth rate, is perhaps the most fundamental piece of information necessary for diagnosing and recovering any species of

concern. Managers and researchers commonly use simple series of abundance data collected over time, without count covariates and ignoring density dependence, to address the question: "How well is my population doing?". We use simulations to evaluate two commonly-used and one new method to estimate trend parameters (mean and standard error). Surprisingly, we find that the most-commonly used method -- a linear regression of log-transformed count values plotted against time - shows mediocre performance under realistic conditions with both environmental noise and observation error affecting the trend in the time series. The new state space model, which accounts for both forms of variation, performs well in all cases, no matter whether observation error only, environmental variation only, or both are present. These results hold even with missing observations in the time series. We conclude that the dominant paradigm for estimating simple exponential growth through a log-linear regression be strongly tempered by a more thoughtful consideration of its fundamental assumptions. Further, for a fixed budget for field data collection to estimate trend, we recommend directing more effort into fewer, better estimates of abundance, even if some years of sampling must be skipped.

5. SOCIETY FOR CONSERVATION BIOLOGY, CHATTANOOGA, TN, JULY 2008

TITLE: METAPOPULATION VIABILITY OF THE GOLDEN-CHEEKED WARBLER UNDER A CONSERVATION INCENTIVE PROGRAM

AUTHORS: Katherine M. Strickler (presenting author), University of Idaho; Jon S Horne, University of Idaho

ABSTRACT: Conservation incentive programs seek to balance the need to manage endangered species on private lands with concerns about private property rights and conservation costs. We conducted a metapopulation viability analysis to evaluate and inform a conservation incentive program initiated by the Department of Defense, the Recovery Credit System (RCS) for golden-cheeked warblers (GCWA, *Dendroica chrysoparia*) on Fort Hood, Texas. The RCS provides Fort Hood with recovery credits for funding conservation of GCWA habitat on private lands. Recovery credits accumulated by Fort Hood through contracts with private landowners would be used to offset any unanticipated loss of GCWA habitat within the boundaries of the installation. The success of the RCS hinges on the idea that any loss of habitat on Fort Hood can be offset by conserving off-post habitat of equal recovery value. Our objective for this analysis was to quantify the importance of off-post habitat patches for the GCWA metapopulation. We developed software to model metapopulation dynamics and apply recently introduced methods for sensitivity analysis of complex models. Using available demographic and habitat data, we quantified the relative importance of within- vs.

among-patch parameters to population persistence as well as quantifying the relative importance of various patches within the metapopulation. Our results will help determine the recovery value of individual patches in the GCWA RCS.

6.   SOCIETY FOR CONSERVATION BIOLOGY, CHATTANOOGA, TN, JULY 2008

TITLE: USING GENERALIZATIONS DEVELOPED FROM EXISTING DEMOGRAPHIC DATA TO GUIDE MANAGEMENT FOR DATA-POOR SPECIES

AUTHORS: Cynthia Hartway (presenting author), University of Montana; L. Scott Mills, University of Montana; Matthew Kauffman, University of Wyoming

ABSTRACT: Lack of data presents a significant barrier to designing effective management plans for sensitive species. Management interventions are costly and time consuming, yet managers must often make decisions without good evidence that their efforts will increase population performance. Can the demographic responses of past efforts and perturbations guide the management of data-poor species? We addressed this question by conducting meta-analyses on data culled from 147 studies to determine the ability of six common management practices to increase survival and reproduction across multiple taxa. Results indicate that broad generalizations can be made about the effectiveness of some management actions. For example, studies of bird reproductive success indicates that, on average, predator removal programs increase nest success by 41%, whereas habitat alteration through controlled burning increases nest success by 20%, and cessation of grazing generally has no effect. Furthermore, in some cases, variability in the demographic effect of management can be explained by ecological factors: nest success of tree-nesting birds experience a significantly greater boost following predator removals than do ground-nesting species. These meta-analyses results can be combined with demographic models to prioritize on-the-ground actions that most efficiently increase population growth and persistence for species of concern.

7. ECOLOGICAL SOCIETY OF AMERICA ANNUAL MEETING, MILWAUKEE, WI, AUGUST 2008

TITLE: ESTIMATING ECOLOGICAL TREND: WHICH MODEL SHOULD I USE?

AUTHORS: Brian Dennis (presenting author), University of Idaho; Jean-Yves Humbert, ART Research Station, Zurich; L. Scott Mills, University of Montana; Jon S. Horne, University of Idaho

ABSTRACT: Regression of log-abundance of a population versus time is often used to estimate the population's trend. It is not widely realized that such regression carries implicit assumptions about how the trend and the variability in the population abundances arise. If the statistical model does not adequately describe the process by which the data are produced, the trend estimate can be seriously in error. Here we describe three models for estimating population trend. The three are different stochastic versions of the exponential growth model: (1) observation error only, (2) environmental process noise only, and (3) a state space model which combines both observation error and process noise. We describe the statistical methods for obtaining parameter estimates, including estimates of trend, for time series abundance data under each of the three models. Log-abundance regression turns out to correspond to deterministic exponential growth with observation error only, that is, model (1).

8. ECOLOGICAL SOCIETY OF AMERICA ANNUAL MEETING, MILWAUKEE, WI, AUGUST 2008

TITLE: WHAT STATISTICS DO LITERATE ECOLOGISTS NEED TO LEARN, AND IS THERE A BEST WAY TO LEARN THEM?

AUTHORS: Aaron M. Ellison (presenting author), Harvard University; Brian Dennis, University of Idaho.

ABSTRACT: Twenty-first century Ecology requires statistical literacy. Observational studies routinely gather multivariate data at many spatiotemporal scales and experimental studies routinely include multiple blocked and nested factors. Our journals are replete with likelihood and state-space models, Bayesian and frequentist inference, and complex multivariate analyses, and publish papers on statistical theory and methods. We test hypotheses, model data, and forecast future environmental conditions. And many statistical methods cannot be automated in software packages. Developing statistical literacy among ecologists requires overcoming challenges in recognition and understanding. First, we must recognize that fundamental ecological theories are best

phrased in terms of stochastic differential-equation models, but our textbooks have not yet caught up with these models. Second, we must understand statistical modeling well enough to construct, or collaborate with statisticians who construct, nonstandard statistical models and apply various types of inference – estimation, hypothesis testing, model selection, and prediction – to our models and scientific questions. How can ecologists successfully meet these challenges when teaching and learning statistics? Ecologists must first appreciate that statistics is a mathematically-based research discipline and that statistical tools evolve; it is neither a static entity nor an off-the-shelf toolkit. Some ecologists will keep up with the statistical literature and keep their students and colleagues abreast of changes in the field. Others will establish fruitful collaborations with these statistically-aware ecologists or with professional statisticians. We expect that the collaborative approach will be more common. Thus, we suggest that literate ecologists at a minimum should master core statistical concepts, including probability and likelihood, principles of data visualization and reduction, fundamentals of sampling and experimental design, the difference between design-based and model-based inference, model formulation and construction, and basic programming. Because mathematics is the language of statistics, familiarity with essential mathematical tools – matrix algebra and especially calculus – is a must and will facilitate collaborations between ecologists and statisticians. Our experience suggests that statistical concepts are best illustrated in computational laboratories using a diversity of real datasets whose analysis requires different models and approaches. Students must learn statistical concepts before their study designs have been finalized and the data have been collected. Pilot studies are ideal case-studies to use to illustrate statistical concepts, and their analysis can lead to refinements in full-scale design and subsequent analysis. Our experience suggests that students benefit most from statistics courses taught jointly by teams of statisticians and ecologists.

9. XIth INTERNATIONAL GROUSE SYMPOSIUM, WHITEHORSE, YUKON TERRITORY, CANADA, SEPTEMBER 2008

TITLE: ALLEE AND RICKER EFFECTS ON PERSISTENCE OF GREATER SAGE GROUSE POPULATIONS

AUTHORS: E.O. Garton, University of Idaho; Jon S. Horne, University of Idaho; Katherine M. Strickler, University of Idaho; Ann Moser, Idaho Department of Fish and Game; Brian Dennis, University of Idaho; J.W. Connelly, Idaho Department of Fish and Game; Michael A. Schroeder, Washington Department of Fish and Wildlife; J. Michael Scott, USGS.

ABSTRACT: The Allee effect, or declining per capita growth rates at low population sizes, could negatively impact the persistence of declining populations of Greater Sage Grouse (*Centrocercus urophasianus*) while the Ricker effect, declining per capita growth rates at higher population sizes produces an objective carrying capacity for stable or increasing populations. We estimated the parameters of a discrete-time, stochastic growth model incorporating both the Allee and Ricker effects from annual lek counts in the Snake River Plain, Idaho and eastern Washington 1965- 2003. These data provide highly significant evidence for both the Allee and Ricker effects in sage grouse populations. The model provides clear criterion for defining a lower threshold for numbers attending leks below which the populations are likely to decline to extinction. Using this threshold and estimated parameters for the stochastic growth model we could evaluate the probability of persistence or extinction of populations and metapopulations of sage grouse throughout their range. Applying the model to populations varying stochastically at the upper end of the abundance continuum provides a way to evaluate factors influencing carrying capacity of grouse. Sensitivity analysis can be applied to this model and to stage-structured models of sage grouse populations to identify management actions most likely to reverse the long-term declines of the species throughout the west and predict the probable impacts of global climate change.

10.   AMERICAN ORNITHOLOGISTS' UNION, ONE HUNDRED AND TWENTY SEVENTH STATED MEETING, PHILADELPHIA, PA, AUGUST 2009

TITLE: CONSERVATION RELIANT SPECIES: OUR NEW RELATIONSHIP WITH NATURE

AUTHOR: J. Michael Scott, USGS

ABSTRACT: The recovery (delisting) of a threatened or endangered species is often accompanied by the expectation that conservation management of the species will no longer be necessary. However, the magnitude and pace of human impacts on the environment make it unlikely that substantial progress will be made in delisting many species unless the definition of "recovery" includes some form of active management. Preventing de-listed species from again being at risk of extinction may require continuing, species-specific management actions. I characterize such species as "conservation-reliant", and suggest that viewing "recovery" as a continuum of states rather than as a simple "recovered/not recovered" dichotomy may enhance our ability to manage such species within the framework of the Endangered Species Act. With ongoing loss of habitat, disruption of natural disturbance regimes, and the increasing impacts of non-native invasive species, it is probable that the number of conservation-reliant species will increase.

Using Sensitivity Analysis of Population Viability Models to Guide Management Decisions

2008 Annual Meeting of The Wildlife Society

November 8 2008

Hyatt Regency, Miami, Florida

Drs. Jon S. Horne[1], Edward O. Garton[1], and L. Scott Mills[2]

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DETAILED TOPICAL OUTLINE

Approximate Schedule
8:00 am
      Welcome and introduction
8:15 am
      L. Scott Mills: Population Viability Models: History of concept and approaches
            Count-based (**Jon S. Horne)**
                  Density independent growth
                        Observation error
                        Process noise
                        State-space (observation error and process noise)
                  Density dependent growth
                        Ricker (logistic)
                        Gompertz
                        Theta-logistic
                  Models with environmental covariates
             Demographic-based Growth models (**E. O. Garton)**
                  Deterministic single population (DSP) matrix models
                  Stochastic single population (SSP) matrix models
                  Stochastic metapopulation (SMP) matrix models

10:00 am
      BREAK
10:15 am
      LSM: Methods for Sensitivity Analysis of Ecological Models
            Classic approaches
                  Manual perturbation
                  Sensitivity and Elasticity
                  Life Table Response Experiment
             Variance Partitioning (**EOG**):
                  Life Stage Simulation Analysis (**LSM**)
                  Standardized Regression Coefficients
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10:45 am
      JSH: Analytical Tools
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      PopGrowthAnalysis
      RAMAS Metapop (GRIP)
      MetaPVA

11:20 am
      Examples: Sensitivity Analysis of Population Models
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            Case Study: Evaluating patch importance for golden-cheeked warblers (**JSH**)

Population Viability Models

Concept: History
Brief historical tour of PVA concept (see Mills et al. 2005, Ch. 12 Mills 2007):

<u>Minimum Viable Population</u>
1)   Leopold (1933:47):importance of recognizing "the minimum number of individuals which may successfully exist as a detached population."
2)   MVP popularized by injunction from US Congress (NFMA of 1976) to US Forest Service: maintain "viable populations" of all native vertebrate species in each National Forest.
3)   From being a legal / philosophical concept to scientific inquiry:
By late 60's / early 70's: two relevant (but independent) avenues:
a.   demographic (MacArthur and Wilson 1967, Richter-Dyn and Goel 1972) : Critical "floors" for population size, below which population would quickly go extinct. Classic: Shaffer's work on grizzly bear MVP based purely on demo. & environmental stochasticity. (1983, 1985).
b.   Genetic issues
Frankel (1974): Emphasized need and conditions for maintaining evolutionary potential of species: "The prime parameters are the level and distribution of variation, the size of the minimum viable population, and the optimal and minimal sizes of reserves. We need to know the minimum population size which is likely to yield a required level of variation."

4)   Soulé and Wilcox (1980): first specific recommendations for MVP led to famous 50:500 rule.
a.   50: minimum Ne to protect against short-term loss of fitness due to inbreeding, based on empirical observations
Caveats that were often lost:
o   Ne, not N (Ne typically 1/5 to 1/3 N).
o   *short term* guideline for captive breeding and similar "holding operations", not to the long term survival of wild populations which would have many other factors affecting their persistence.
o   based purely on genetic factors, not incorporating the other factors that would again increase the minimum necessary size for persistence.
b.   500: estimated minimum genetic Ne where loss of additive genetic variation of a quantitative character due to genetic drift would be balanced by new variation due to mutations. → Range up to 5,000 or more.

<u>MVP is problematic for both philosophical and scientific reasons.</u>
a) point estimate vs embracing uncertainty
b) ecologically effective versus minimally viable.

Population Viability Analysis

a. Gilpin and Soule (1986): "This chapter introduces the term 'population vulnerability analysis' (PVA) for analyses that estimate minimum viable populations (MVPs). That is, MVP is the product, and PVA the process."

b. By the 1987 <u>Viable Populations for Conservation</u> book: PVA had morphed into "Population Viability Analysis".

c. What is PVA?
   o 'Mills' def.: *the application of data and models to estimate probabilities that a population will persist for specified times into the future (AND to give insights into factors that constitute the biggest threats).*

<u>Defining and describing "extinction":</u>
   Quasi-extinction threshold advantages
   o Provides a lot more options than modeling for extinction!
   o Allows you to finesse around the ignorance of how dynamics will change for your species at very low numbers (e.g., genetic stochasticity, demographic stochasticity, Allee affects, etc.).

<u>"Extinction Vortex"</u> (from Mills 2007)

Fig. 12.1 A simplified representation of the extinction vortex. The effects of deterministic stressors are filtered by the population's environment (habitat as well as variable extrinsic factors such as weather, competition, predators, and food abundance) and by its structure (including age structure, sex ratio, behavioral interactions, distribution, physiological status, and intrinsic birth and death rates). Each turn of the feedback cycle increases extinction probability (Gilpin & Soulé 1986). The extinction vortex model predicts that some small populations are more likely to become smaller and eventually go extinct with each generation due to the interaction of genetic and nongenetic factors. Modified from Soulé and Mills (1998). Copyright (1998) AAAS.

Two Primary Ways of Conducting a PVA

1) Count-based (i.e., time series of abundance)
2) Demographically explicit (based on vital rates)

Count-based population growth models

Population Growth in Unlimited Environments

- Overview (see Mills 2007:91 - 99)

Deterministic Exponential Growth Model

- Unlimited, constant, favorable environment (i.e., population growth rate remains constant).

- Age-specific birth and death rates remain constant (i.e., population has a stable-age distribution).

Discrete growth:
$$N_{t+1} = N_t \, \lambda$$
If the population continues to grow at the rate λ for "t" time steps from an initial abundance at time 0 (N_0), then at time t we would expect N to be:
$$N_t = N_0 * \lambda_1 * \lambda_2 * \ldots \lambda_t$$
$$N_t = N_0 \, \lambda^t$$

Stochastic Exponential Growth Models (see Humbert et al. *in review*):

- **Stochastic:** involving a random variable; a random outcome

- A **random variable** (e.g., number of offspring) is one that can take more than one value in which the values are determined by probabilities.

- **Statistical Distributions** and random outcome (Examples: uniform, normal, log-normal)

A reminder on calculating geometric mean, and why λ_G is less than λ_A:

The geometric mean differs from the arithmetic mean because instead of adding a bunch of numbers and dividing by the total, you instead multiply a bunch of numbers (let's call it "t" numbers) and take the tth root of the product. To put these words into an equation for the geometric mean population growth rate (λ_G) over time:

$$\lambda_G = \sqrt[t]{(\lambda_1 * \lambda_2 * \lambda_3 * \ldots \lambda_t)} \text{ or equivalently}$$

$$\lambda_G = \left(\lambda_1 * \lambda_2 * \lambda_3 * \ldots \lambda_t\right)^{\frac{1}{t}}$$

The geometric mean will be less than the arithmetic mean when there is stochasticity. Let's run through an example. Suppose an endangered population grows at a constant $\lambda=1.05$; we would expect a 5% increase per year, so that in 16 years a population of 100 would have an expected size of

$$N_{16} = 100 * 1.05^{16} = 218$$

Now suppose instead that the population growth alternated each year between $\lambda = 1.55$ and $\lambda = 0.55$. The arithmetic mean of the growth rate is still 1.05 [from (1.55+0.55)/2]. But the growth of the average population is governed by the geometric mean which is

$$\sqrt{1.55*0.55} = 0.923.$$

After 16 years, the expected population size would be

$$N_{16} = 100 * 1.55^8 * 0.55^8 = 28.$$

This is the same as projecting all 16 years with the geometric mean: $100 * 0.923^{16} = 28$.

A population of 28 is a lot less than the 218 expected from the arithmetic mean! The variation in population growth leads to a likely decline for the population, even though the deterministic growth rate implies that the population should increase substantially.

An equivalent way to calculate the geometric mean population growth rate from a time series takes advantage of the mathematical properties of good old [$r=\ln(\lambda)$]:

> a) Calculate r for each interval by $\ln(N_{t+1}/N_t)$.
> b) Take the arithmetic mean of all of the r's to obtain $\bar{r}$.
> c) Convert the $\bar{r}$ back to λ (by way of $\lambda = e^r$) and you've got your λ_G.

Another way to see the phenomenon (from Mills 2007):

Fig. 5.5 Stochastic geometric growth showing 25 possible population growth trajectories for hypothetical snail kite populations (e.g. Beissinger 1995) beginning with 10 individuals. For each replicate, λ at each of 20 time steps varied randomly between 0.5 and 1.7 ($\sigma_\lambda^2 = 0.12$). λ_A is therefore 1.1 and λ_G approximately 1.05 (represented by thick lines). Because λ_G represents median population growth, about half of the final abundances fall above the λ_G line and half below.

<u>Model 1: Exponential Growth Observation Error (EGOE)</u>

o   The oldest, and most predominantly used model results in a log-linear regression of counts against time, where the slope of the regression gives the population trend (e.g. Caughley 1977, Eberhardt and Simmons 1992, Gerrodette 1987)

o   Actual population growth is *deterministic*

o   Stochasticity arises only from imprecision of abundance estimates

$$Y_t = \ln(N_0) + \mu t + E$$

where, Y_t = natural logarithm of observed (estimated) abundance; μ = instantaneous growth rate; $E \sim N(0, \tau^2)$

**Note: estimates of μ and τ can be obtained by linear regression of $\ln[n_t]$ against time (t).

$$\hat{n}_0 = Exp[\text{y-intercept}]$$

$$\hat{\mu} = \text{slope}$$

$$\hat{\tau}^2 = \text{mean residual sum-of-squares}$$

Model 2: Exponential Growth Process Noise (EGPN)

- o   Model often used to analyze population viability based on the exponential growth model (see Dennis et al. 1991, Cha. 3 Morris and Doak 2002)

- o   Actual population growth is stochastic

- o   'Process' noise: environmental stochasticity bumps the population growth rate around at each time step

$$\ln\left(N_{t+1}\right) = \ln\left(N_t\right) + \mu + F$$

where, $F \sim N\left(0, \sigma^2\right)$

- •   Parameters can be estimated (see Dennis et al. 1991) by linear regression, without intercept, of $y_i = \left[\ln(n_i / n_{i-1})\right]/\sqrt{s_i}$ as the 'dependent variable' and $\sqrt{s_i}$ as the 'independent variable'. Where, $s_i = t_i - t_{i-1}$

Model 3: Exponential Growth State Space (EGSS)

- o   Actual population growth is stochastic

- o   'Process' noise and observation error induce stochasticity

$$\ln\left(N_{t+1}\right) = \ln\left(N_t\right) + \mu + F$$ actual abundance

$$Y_{t+1} = \ln\left(N_{t+1}\right) + E$$ natural logarithm of observed abundance

- o   Parameters can be estimated (see Staples et al. 2004) using maximum likelihood or restricted maximum likelihood (REML) . It has been our experience that REML estimates perform better.

Population Growth in Limited Environments

- Limited environments cause age-specific birth and/or survival rates to **decline** with increasing population size.

- Intraspecific competition causes growth rates to decline with increasing population size

Stochastic Logistic (Ricker) Growth Model

- Growth rate is a **decreasing <u>linear</u>** function of population size

$$\ln\left(N_{t+1} / N_t\right) = a + bN_t + F$$

where, a = maximum growth rate at $N = 0$ (i.e., *Rmax*); b = effect of intraspecific competition

**Note if $b = 0$, this is the EGPN model

Stochastic Gompertz Growth Model

- Growth rate (i.e., birth rate and mortality rate) is a **decreasing <u>linear</u>** function of the **natural logarithm** of population size

$$\ln\left(N_{t+1} / N_t\right) = a + b \times \ln\left(N_t\right) + F$$

**Notice: *a* can no longer be interpreted as *Rmax*… As *N* approaches 0, the growth rate approaches infinity (∞). *a* is the growth rate when abundance = 1.

Stochastic Theta-logistic Growth Model

- Growth rate (i.e., birth rate and mortality rate) is a **decreasing <u>linear</u>** function of population size **raised to the power theta** (θ)

$$\ln\left(N_{t+1} / N_t\right) = a + bN_t^{\theta} + F$$

Three situations arise:

1) $\theta = 1$: Ricker (logistic)-type density dependence

2) $0 < \theta < 1$: Growth rate versus *N* is a concave relationship (e.g., Gompertz)
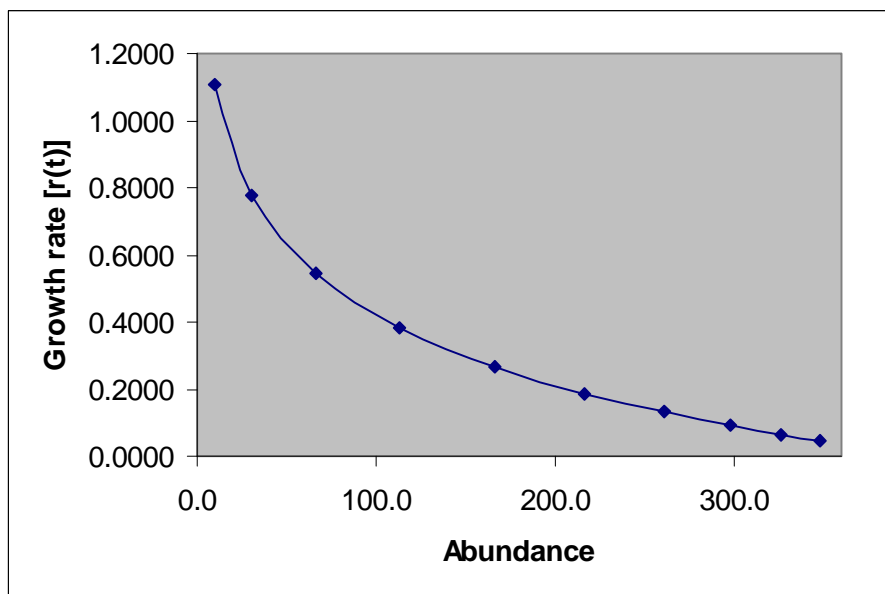
3) $\theta > 1$: Growth rate versus *N* is a convex relationship

Demographic-based population growth models

Population projection matrix

A *population projection matrix* is "…merely a box to help us keep straight the bookkeeping of birth and survival, a mathematical representation of biological processes." (from Mills 2007).

Fig. 7.1 Anatomy of a female-based projection matrix, using as an example the common frog (Biek et al. 2002; see also Box 4.8). This species has three stages: pre-juvenile (first year, consisting of the embryo, tadpole, and overwintering metamorph), juvenile (next 2 years), and adult. The projection interval, or time step, for this matrix is 1 year. The first row represents reproduction from each stage to the next year. The diagonal (e.g. $a_{2,2}=0.25$ and $a_{3,3}=0.43$; see text for an explanation of this notation) represents the proportion of individuals in a stage that will survive and still be in the same stage next year, while the subdiagonal (just below the diagonal; e.g. $a_{2,1}=0.024$ and $a_{3,2}=0.08$) represents the proportion surviving and advancing to the next stage next year.

How timing of sampling affects the matrix (from Mills 2007)
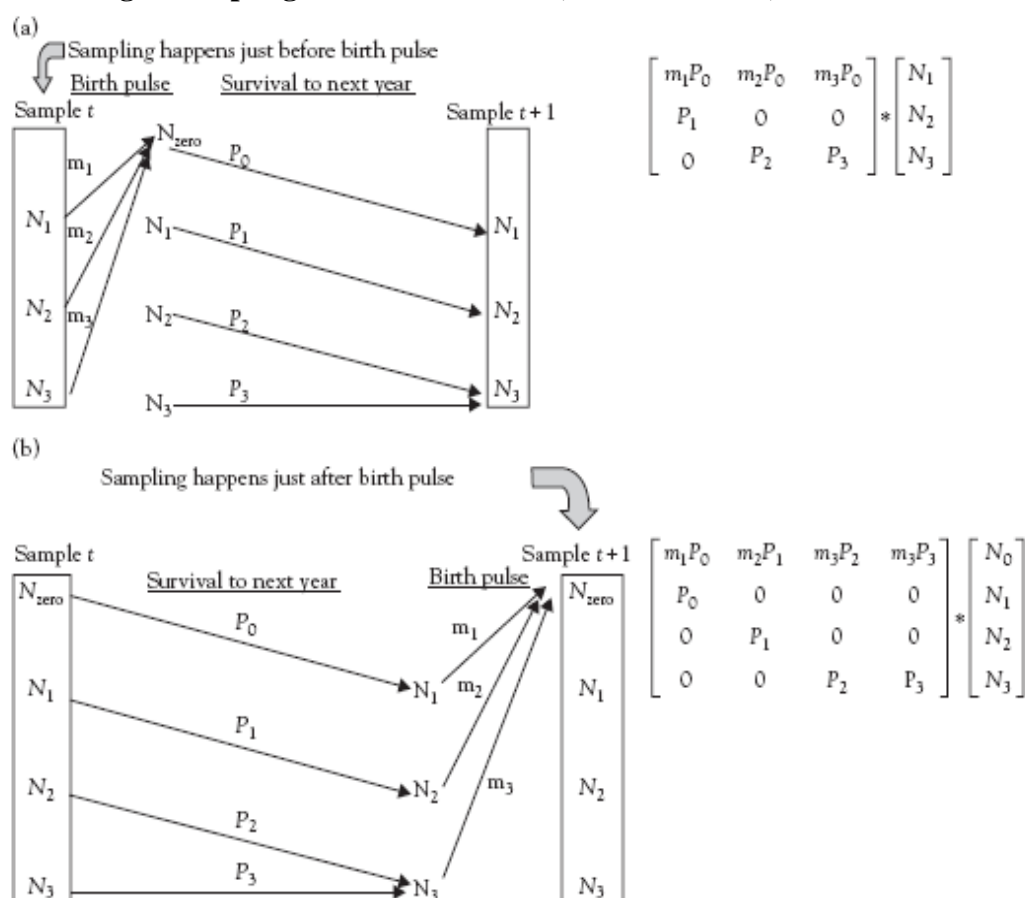
Fig. 7.2 General schematics of the birth and death processes captured when the sampling is either (a) before the birth pulse or (b) after the birth pulse. The animals sampled at times t and $t+1$ are boxed, with N_j representing number of individuals in each stage class j. This example assumes that animals stay in each stage for only one time step, except that those in the last stage can survive and remain in that stage for multiple time steps. Fecundity for each age class (m_j) represents the average number of offspring born to each individual of N_j. The probability of survival through one time step is represented by P_j. To the right of each schematic is the resulting projection matrix and population-size vector. In (a), note that newborns (N_0) are not seen until they have survived through their first year (P_0) to be counted as N_1 at the next sample interval; likewise, individuals in age class 1 (N_1) are just about to become 2 years old, and so on. The next batch of N_0 individuals are born just after sampling. In (b), note that there is an extra column and row in the post-birth-pulse matrix (compared to the case of the pre-birth pulse) because post-birth sampling occurs just after reproduction, making N_0 recognizable as its own class.

Projecting a matrix through time

$$\mathbf{n}(t+1) = \mathbf{M}*\mathbf{n}(t)$$

Matrix x Vector multiplication conveniently carries out the required mathematical operations (addition due to births and subtraction due to mortality) to project each age (stage) to the next time step (from Mills 2007)

Fig. 7.3 A real-life example of a female-based post-birth-pulse matrix model for the common frog (Fig. 7.1). Female eggs per adult female refers to fecundity (see Box 4.8). (a) A diagramatic representation of the model; (b) the matrix (try plugging in the values and make sure you get the matrix in Fig. 7.1). Note that the matrix shows reproduction for juveniles (row 1, column 2) as well as adults (row 1, column 3) because a portion of the juveniles transition during the time step to become adults, at which point they reproduce. In general, for post-birth-pulse models for iteroparous species with n reproductive stages there should be $(n+1)$ non-zero elements in row 1.

$$
\begin{array}{ccc}
\text{The matrix} & * & \begin{array}{c}\text{Population vector}\\\text{in 2003}\end{array} & = \\
\begin{bmatrix} 0 & 52 & 279.5 \\ 0.024 & 0.25 & 0 \\ 0 & 0.08 & 0.43 \end{bmatrix} & * & \begin{bmatrix} 70 \\ 20 \\ 10 \end{bmatrix} & = & \begin{bmatrix} (0*70)+(52*20)+(279.5*10) \\ (0.024*70)+(0.25*20)+(0*10) \\ (0*70)+(0.08*20)+(0.43*10) \end{bmatrix} & = \\
& & N_{2003}=100 & & &
\end{array}
$$

$$
\begin{array}{cc}
& \begin{array}{c}\text{Population vector}\\\text{in 2004}\end{array} \\
& \begin{bmatrix} 3835.00 \\ 6.68 \\ 5.90 \end{bmatrix} \\
& N_{2004}=3848
\end{array}
$$

Repeat multiplying the matrix by the current vector to get

$$
\begin{array}{cccc}
& \text{Population vector in 2005} & & \text{Population vector in 2006} \\
\rightarrow & \begin{bmatrix} 0+347.36+1649.05=1996.41 \\ 92.04+1.67+0=93.71 \\ 0+0.53+2.54=3.07 \end{bmatrix} & \rightarrow & \begin{bmatrix} 5731.38 \\ 71.34 \\ 8.82 \end{bmatrix} \\
& N_{2005}=2093 & & N_{2006}=5812
\end{array}
$$

Fig. 7.4 An example of how to project a matrix through time. The sample matrix comes from the common frog (see Figs 7.1 and 7.3). A matrix of mean vital rates is projected for three time steps, beginning in the year 2003. Initially, our population has 70 pre-juveniles, 20 juveniles, and 10 adults. At the bottom of each vector is the total population size (N) for that year, rounded to the nearest whole female animal (as this is a female-based matrix).

Stochastic matrix models

**Remember: *Stochasticity* involves a *random* outcome

Two types of stochasticity

1)   Environmental: random outcomes for survival and reproduction in each time step of the projection model (i.e., temporal stochasticity).
   - Environmental stochasticity affects the entire population
   - Modeled as random draws at each time step for survival and reproduction given means and variances for these rates

2)   Demographic: Each individual has its own random fate
   - Survival – Each individual either lives or dies according to a binomial process
   - Reproduction – The actual number of offspring by each individual is a random variable (e.g., Poisson process)

Metapopulation models

- Most metapopulation models use stochastic matrix models as the basis for each population's growth with the addition of dispersal among populations and correlated demographic rates among populations

Hierarchically structured biological units based on demography, movements, genetics and geography:
- Individuals
- Demes
- Populations
- Metapopulations

Metapopulation Structures

- Non-equlibrium

- Classic

- Patchy

- Mainland-Island/Source-Sink

Examples:

- Red-winged Blackbirds in SE Washington

- Greater Sage Grouse

Sensitivity Analysis of Ecological Models

Critical to determining the effects that various components within a population projection model will have on overall viability are methods for determining the relationship between changes in model components and changes in population viability. Sensitivity analysis offers a direct avenue for quantifying these relationships by assessing how the output from a given model responds to changes in its inputs (Saltelli et al. 2000). Sensitivity analysis includes a wide range of methods that can be grouped into 2 general approaches including local sensitivity analysis and global sensitivity analysis (Saltelli et al. 1999). In local sensitivity analysis, model parameters are varied one at a time by a fixed amount while others are held to their nominal (i.e., best estimate) value. Local sensitivity to a parameter is measured by relating changes in the model output to the change in the parameter (sometimes normalized by the nominal value or standard deviation). Local sensitivity analysis has seen widespread use and because sensitivity values can usually be derived analytically through the use of partial derivatives, implementation is often straightforward. However, local measures of sensitivity can suffer when changes in parameters cause non-linear responses in the model output, when parameter uncertainty is not sufficiently characterized by a fixed change in the nominal value, when it is realistic to consider simultaneous changes in other model parameters, or when parameters interact. Many of these problems can be alleviated by employing a global approach to sensitivity analysis.

Two broad categories of sensitivity analyses:
1. Local sensitivity analysis – parameters are changed one at a time around the 'local' or best estimates (e.g., manual perturbation, analytical sensitivity/elasticity analysis)
2. Global sensitivity analysis – multiple parameters can be varied simultaneously and over a range of values (e.g., life-stage simulation analysis, variance partitioning).

Global sensitivity analysis differs from local sensitivity analysis in two important ways. First, the full range of possible values for a parameter is explored to determine its effect on model output. Second, effect of the focal parameter on model output is averaged over possible variations of other model parameters. Because of the difficulty in relating model output to simultaneously varying and interacting inputs, several methods have been developed for global sensitivity analysis (Saltelli et al. 2000).

Using sensitivity analysis to inform conservation decisions based on population projection models has become increasingly popular and sophisticated. One of its earliest uses was in evaluating life-history characteristics of California condors that make the species particularly vulnerable to extinction (Mertz 1971). This study used manual perturbation, a form of local sensitivity analysis, to change vital rates and evaluated the effect these changes had on the likelihood of the population's persistence. Manual perturbation continues to be a popular method for conducting a sensitivity analysis on PVA models. However, several alternative approaches (see Mills and Lindberg 2002 for a review) have been developed including analytical sensitivity and elasticity analysis (Goodman 1971, Caswell 2001); life-table response experiments (Caswell 1989); and regression-based approaches (McCarthy et al. 1996, Wisdom and Mills 1997, Wisdom et al. 2000).

Classic Approaches: Importance of Vital Rates

Background:

- Within a population, different stage or age classes contribute differentially to future population growth. This can be quantified by a stage's "Reproductive Value":

For example (from Mills 2007):

Fig. 7.6 A demonstration of reproductive value by projecting common frog population size beginning with 100 adults, 100 juveniles, or 100 pre-juveniles, with the constant vital-rate matrix from Fig. 7.1. Although the initial abundance, the projection matrix, and eventual population growth rate and SSD are identical in each case, the initial stage distribution causes bounce in population growth early on, and leads to drastic differences in abundance. Reproductive value is typically scaled relative to the first age class. The right side of the grap shows how reproductive value can be calculated based on relative abundances at SSD, dividing each abundance by that of the population begun with the first age class. (I used abundances in year 2017, after 14 years had passed, but you could use abundances any time after SSD was achieved.)

- At the same time, we know that different stage or age classes vary in their proportional representation in the population; we quantify that by the "Stable Age Distribution". (from Mills 2007)
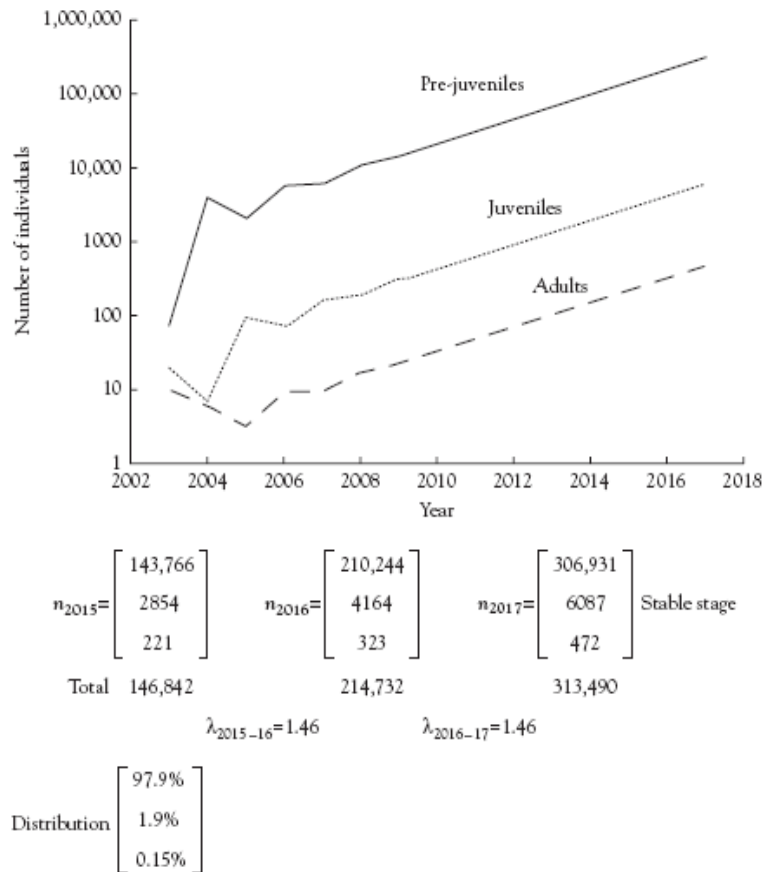
$$n_{2015}=\begin{bmatrix} 143{,}766 \\ 2854 \\ 221 \end{bmatrix} \quad n_{2016}=\begin{bmatrix} 210{,}244 \\ 4164 \\ 323 \end{bmatrix} \quad n_{2017}=\begin{bmatrix} 306{,}931 \\ 6087 \\ 472 \end{bmatrix} \text{Stable stage}$$

Total 146,842   214,732   313,490

$$\lambda_{2015-16}=1.46 \quad \lambda_{2016-17}=1.46$$

$$\text{Distribution}\begin{bmatrix} 97.9\% \\ 1.9\% \\ 0.15\% \end{bmatrix}$$

Fig. 7.5 Convergence to a SSD for the common frogs considered in previous figures. Population numbers over 14 years (from 2003 to 2017) are shown by stage class. The number of frogs is plotted on a logarithmic scale to accommodate the huge numbers of pre-juveniles, and because at SSD the trajectories become linear. Below the graph are the vectors (**n**), total population sizes, and geometric growth rates (λ) for the final 3 years. When the population reaches SSD, both the population growth rate (λ) and the proportion of individuals in each stage remain constant.

- So if different stage classes have different impact on future population growth, and are differentially represented in the total population, it makes sense that different vital rates associated with those stages would have different effects on population growth!
- Next, the 4 primary ways that the "importance" of different vital rates have been quantified via "sensitivity analysis"

Method #1: Manual perturbation

Perturb or change the value of a parameter in a population growth model and see how the change affects the output.

- Growth models based on time series: Change the growth rate; the effect of density dependence or the amount of environmental stochasticity
- Demographic-based growth models: Change survival, fecundity or the variance in these parameters

Method #2: Analytical sensitivity and elasticity analysis

Classically applied to matrix projection models (from Mills 2007)

sensitivity for a vital rate that makes up matrix element $a_{i,j}$ (remember this is the matrix element in row i and column j) is a function of the reproductive value of the age class (v_i) and the SSD (w_j)[8]:

$$\text{Sensitivity of matrix element } a_{i,j} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\left(\sum_{k=1}^{\text{Last stage class}} v_k w_k \right)} \qquad (7.2)$$

$$\text{Elasticity of matrix element } a_{i,j} = (\text{sensitivity of } a_{i,j}) * \frac{a_{i,j}}{\lambda} \qquad (7.4)$$

BUT IN THE REAL WORLD WE KNOW THAT BOTH NATURE AND MANAGEMENT CHANGE DIFFERENT VITAL RATES BY DIFFERENT AMOUNTS. SO WE NEED TO ACCOUNT FOR THE MAGNITUDE, OR VARIATION, OF VITAL RATE CHANGES.

Method #3: Life table response experiments (LTRE)

Provides a way of incorporating variation in vital rates into sensitivity/elasticity analysis (see Caswell 2001). However a more flexible method for incorporating variation is 'Life-stage simulation analysis' (see next section).

Method #4: Life-stage simulation analysis (LSA)

Vital rates with low elasticities that vary a lot can affect population growth more than those that change little.

1. Construct replicate matrices using vital rate means and variation

2. Project each of the 1,000 or so matrices to stable age distribution

3. For each set of vital rates, calculate finite growth rate (λ)

4. Calculate coefficient of determination (r^2) from regression of λ on each vital rate

SOME EXAMPLES OF SENSITIVITY ANALYSIS IN ACTION TO HELP GUIDE
WILDLIFE MANAGEMENT DECISIONS (SEE MILLS ET AL. 2007, CHAPTER 7 IN
BACK OF YOUR PACKAGE)

EXAMPLE 1 (from Mills 2007): what is the best way to *decrease* population growth of an
invasive or pest species? (brown-headed cowbird)
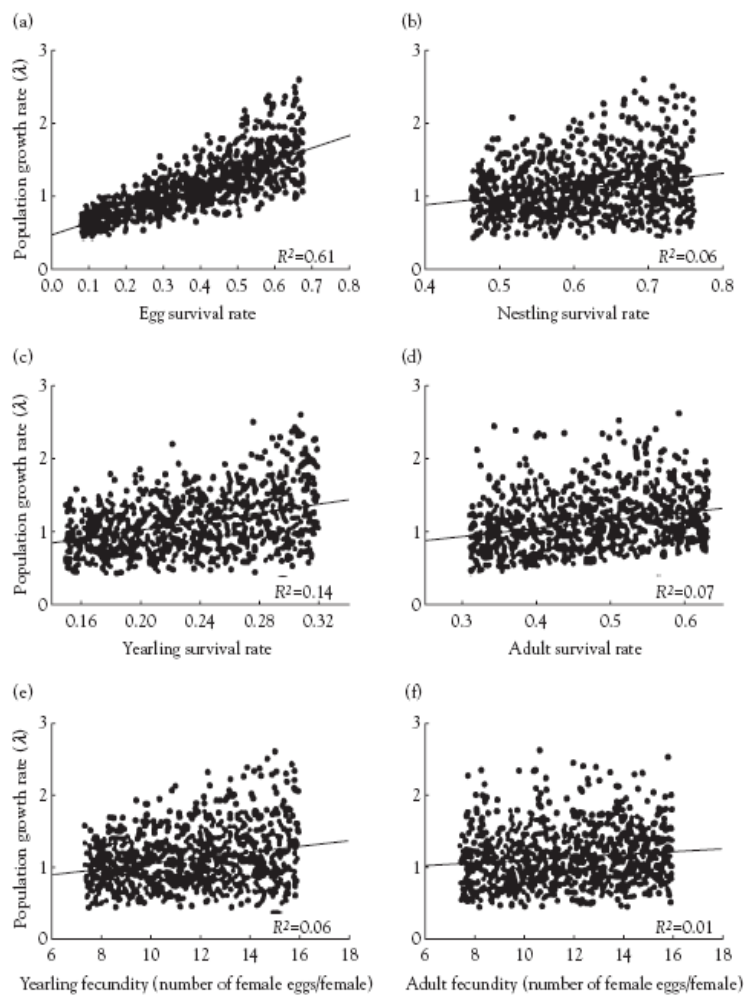
Fig. 7.9 An LSA-based approach to evaluating the relative importance of different vital rates to
population growth in brown-headed cowbirds. The R^2 value describes the proportion of varia-
tion in λ explained by variation in a vital rate, based on 1000 simulated matrices where vital
rates were chosen from the range of variation determined from published studies. Notice that
egg survival alone accounts for 61% of the variation in λ. From Citta & Mills (1999)

EXAMPLE 2 (from Mills 2007): How should $50 million in Duck Stamp dollars be used to maximize population growth of a harvested species? (mallards)

Mid-continent mallard population: percentage contribution to variation in λ

Nest success ($R^2=0.43$)

Breeding incidence ($R^2=0.004$)

Egg hatch rate ($R^2=0.004$)

Clutch size ($R^2=0.02$)

Nonbreeding survival ($R^2=0.09$)

Renesting intensity ($R^2=0.05$)

Total R^2 (excluding nonbreeding survival) =0.84

Duckling survival ($R^2=0.14$)

Breeding season survival ($R^2=0.19$)

Fig. 7.10 Results of an LSA analysis for female mid-continent mallards in North America (Hoekman et al. 2002). Each pie slice shows the proportion of variance in population growth rate explained by that vital rate in 1000 simulations of vital rates drawn from field studies. In other words, the plot shows the R^2 from regression plots of vital rates against population growth determined as in the cowbird example (Fig. 7.9). Approximately 84% of the variation in population growth rate is expected to arise from breeding-ground vital rates. The 7% not accounted for in the pie can be thought of as statistical noise, accounted for by interactions among the rates and the nonlinear responses of population growth to the changes in vital rates.

EXAMPLE 3 (from Mills 2007): Which management actions would most efficiently increase population growth rate for an endangered species? (red-cockaded woodpecker)

(a)

Transition	From fledglings	From helpers	From floaters	From solitary males	From 1-year-old breeders	From ≥2-year-old breeders
Fledglings produced	0.080	0.266	0.324	0.275	0.486	0.522
To helpers	0.294	0.494	0.000	0.000	0.000	0.000
To floaters	0.031	0.000	0.000	0.000	0.000	0.000
To solitary males	0.043	0.020	0.172	0.216	0.000	0.000
To 1-year-old breeders	0.074	0.000	0.000	0.000	0.000	0.000
To ≥2-year-old breeders	0.000	0.257	0.483	0.410	0.725	0.800

(b) Exponential growth rate vs. Change due to management (%). Legend: Remove invaders; Female translocation; Cavities in occupied territory; Cavities in unoccupied territory.
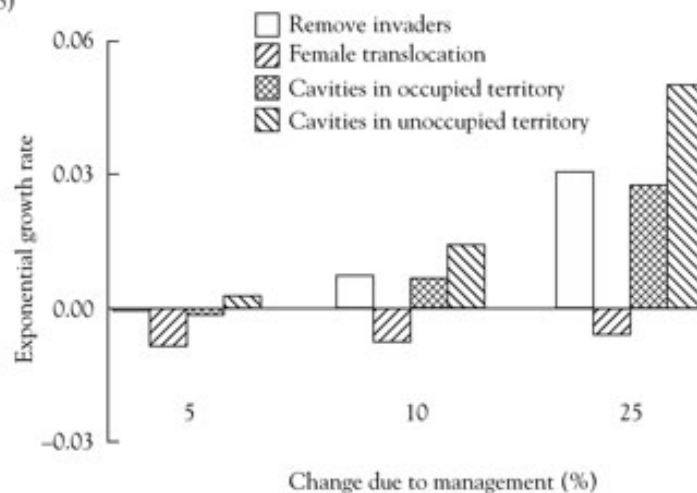
EXAMPLE 4: How should research and management focus efforts to reverse global amphibian population declines?

[see powerpoint presentation: "amphibian example of sensitivity analysis.ppt"

Variance Partitioning

In general, a global sensitivity analysis to partition the output variance involves the following:

1. The possible values for each of the *i* input parameters in a model are characterized by a probability distribution P_i. Often these distributions are chosen to reflect the uncertainty in the parameter estimates but, depending on the goal of the sensitivity analysis, they may reflect natural variation or uncertainty related to the effects of management actions.

2. The population projection model is run for many random draws of the model parameters from their respective probability distributions. Repeated samples are selected from each distribution and these values are used as inputs for model evaluation. A unique model output (e.g., probability of persistence) is calculated for each of the replicate input samples.

3. The distribution of the output (i.e., viability) is described. This step is commonly referred to as "**uncertainty analysis**" because we are depicting the uncertainty in the output that results from uncertain inputs into the model.

4. Sensitivity indices are constructed relating the uncertainty in the model parameters to the uncertainty in the model output. In particular, many metrics for describing sensitivity provide the proportion of the variance in the output attributable to the variance in the input parameters.

5. Each parameter can be ranked in importance according to the proportion of the total variance in the output that is attributable to each parameter.
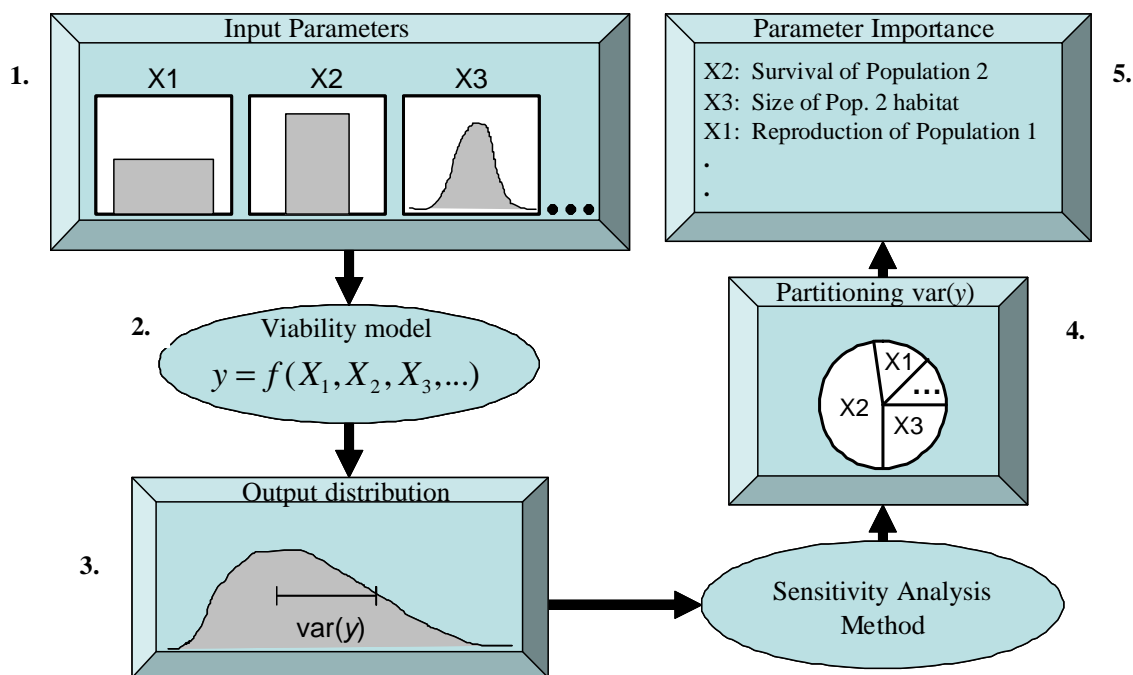
Standardized regression coefficients

The idea behind LSA (i.e., relating the uncertainty in the input parameter values to the uncertainty in the output metric by a linear model) can be generalized for any population projection model (e.g., stochastic models) and for other response variables.

From the model,

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_k X_k + \varepsilon$$

we have,

$$\sigma_Y^2 = \beta_1^2 \sigma_1^2 + \beta_2^2 \sigma_2^2 + \cdots + \beta_k^2 \sigma_k^2 + \sigma_{y.x}^2$$

If the X_is are *independent* (i.e., not correlated) random variables (Snedecor and Cochran 1989:359).

- In this special case, the standardized partial regression coefficients (i.e., $\beta_i \sigma_i / \sigma_Y$) are equal to the correlation coefficients of X_i and Y (Sokal and Rohlf 1981:644).

- $\left(\beta_i \sigma_i / \sigma_Y\right)^2$ (the **squared** standardized regression coefficient) measure the fraction of the variance of Y attributable to its linear regression on X_i. This fraction can reasonably be regarded as a measure of the relative importance of X_i.

Sobol' indices

- Accommodates non-linear relationships between the output metric and the input parameters.
- Allows for interactions among input parameters

The total variance in the output $D = \text{var}(y)$ is decomposed into contributions from each parameter i.

$$D = \sum_{i=1}^{n} D_i + \sum_{1 \le i \le j \le n} D_{i,j} + \cdots + D_{1,2,\ldots,n}$$

where, D_i are the main effects and $D_{i,j}$ are the second (and higher) order interaction effects between i and j, etc.

First order Sobol' indices are given by:

$$S_i = D_i \big/ D$$

Total sensitivity indices are given by:

$$TS_i = S_i + \sum_j S_{i,j} + \cdots + S_{1,2,\ldots,n}$$

Fourier Amplitude Sensitivity Test (FAST)

- Goal is estimation of Sobol' indices (i.e., partition output variance into main and interaction effects)
- Somewhat '*FAST*er' because indices can be achieved with only a single set of runs (as opposed to an alternative Monte Carlo procedure)
- Idea is to fit a Fourier series to the output distribution and relate the input parameters to this function.

Remember:

Sobal' indices and those derived from FAST are considered 'model independent' in that they do not rely on linear or near-linear relationships between the model outputs and the input parameters. They, of course, are not truly model independent but do offer more flexibility than regression-based approaches. Additionally, these methods allow the variance in the output attributable to variation in input parameters to be decomposed into first order effects as well as higher order effects caused by interactions among model parameters. Total effect indices are calculated by summing the first order effects with each additional higher order effects. Thus, they allow for the importance of interactions among model parameters to be quantified in relation to model output.

Analytical Tools (Computer Software)

Recovery Action Prioritization (RAP sheets)

Use Principles of Sensitivity Analysis to Guide Management Decisions When Data Are Sparse

- Created by L. S. Mills, C. Hartway, M. Kauffman
- See: http://www.uwyo.edu/rap_sheets/rapmainpage.html (for the work in progress)

Also see "Rap Sheets for Miami TWS"

PopGrowthAnalysis

Visual Basic Program created by J. S. Horne, B. Dennis, J. Humbert, L. S. Mills, E. O. Garton.

- This program is a user-friendly 'front-end' to interface with the freely available program R (R Development Core Team 2006; program available online).
- Utilizes R contributed package *PopGrowth4*
- Input data can be a tab-delimited text file or a Microsoft Excel spreadsheet
- Allows user to fit several population growth models to time-series abundance data
  - Exponential growth with observation error (EGOE)
  - Exponential growth with process noise (EGPN)
  - Exponential growth state space (EGSS)
  - Ricker (logistic)-type density dependent growth
  - Gompertz density dependent growth
  - Theta-logistic density dependent growth
- Provides selection criteria (Akaike's Information Criteria) for EGPN, Ricker, Gompertz and Theta-logistic growth models
- Provides relevant parameter estimates and measures of precision of these estimates
- Enables user to easily implement *Viable Population Monitoring* (Staples et al. 2005) based on parameter estimates from EGPN and EGSS models
- Provides residuals from fitted models for investigating effects of environmental covariates and assessing correlations among populations

RAMAS MetaPop (GIS)

- Stochastic matrix-based metapopulation projection model (see http://www.ramas.com/)
- Very flexible (i.e., dangerous)
- If the analysis is well thought out, it can be quite powerful
- Also, you can do a sensitivity analysis now with an R Package called *GRIP* (Generation of Random Input Parameters)

GRIP (Generation of Random Input Parameters)

Introduced by Curtis and Naujokaitis-Lewis (2008)

- Generates unique sets of input parameters for replicate stochastic simulations in RAMAS Metapop 4.0
- Utilizes freely available program R (R Development Core Team 2006; program available online)
- R code for executing GRIP is available as a Supplement in (Curtis and Naujokaitis-Lewis 2008) through *Ecological Archives* (A018-033-S1)
- Will likely need to modify R code to conduct relevant/realistic sensitivity analyses for a particular (meta) population

MetaPVA

Visual Basic Program in development by J. S. Horne, J. Tracey and E. O. Garton.

- Initiated (Before GRIP!) to allow users to easily implement several methods of sensitivity analysis
- Based on stochastic metapopulation projection model analogous to that used in RAMAS Metapop
- Utilizes R contributed package *Sensitivity*
- Currently allows more flexibility in how parameters are sampled and automates the sensitivity analysis

Examples: Sensitivity Analysis of Population Models

Wolves and Elk in Yellowstone National Park

An Example of a DSP: Projecting Northern Yellowstone Elk Population Growth and Reintroduced Wolf Population Impacts

- Empirical, stage-based model developed from published studies of Northern Yellowstone elk herd and wolves feeding on moose and deer in other areas
- Validation based on previous history of elk herd and aerial surveys adjusted for visibility bias
- Mortality rates of calves and cows decline with increasing elk population size
- Hunting mortality is additive
- Wolf mortality estimated from functional response of wolves to elk density and handling time
- Wolf mortality is compensatory on cows and reduces average female age
- Long-term persistence of Northern Yellowstone elk herd assured if human harvest not too high and winter severity not too extreme

Elk in the Blue Mountains of Washington

An example of a SSP: Stochastic density dependent model of harvested elk population in Blue Mountains of SE Washington

- Generalized Northern Yellowstone elk-wolf model to apply to other elk populations based on relative size and productivity of summer and winter ranges, preganancy rates of elk, etc.
- Harvest and winter severity treated as stochastic
- Deterministic model predictions validated against aerial surveys and harvest records
- Stochastic model predictions depend upon winter severity and harvest rates by stage class

Golden-cheeked Warblers

- Global sensitivity analysis used to determine importance of patches in golden-cheeked warbler metapopulation
- Based on stochastic demographic-based metapopulation model
- Unintended Consequence: Sensitivity Analysis was helpful in identifying problems in the model *structure*

Key References

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Metapopulations

- **E. Oz Garton & Jon Horne**
- **Fish and Wildlife Department**
- **Jocelyn Aycrigg & Leona Svancara, PhD Candidates**
  - Fish and Wildlife Department
    - University of Idaho
    - Moscow, ID 83844

Overview

- Structure of biological populations and their habitat (spatial structure)
- Red-winged blackbird metapopulation in Columbia NWR in SE Washington
- Elk metapopulation in Idaho
- Greater sage grouse species metapopulation and component populations

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Red-winged Blackbirds

Hierarchic Structure:

Individual
Deme
Population
Metapopulation

Columbia NWR
USFWS Staff,
Gordon Orians,
Les Baletsky &
Robyn Miller
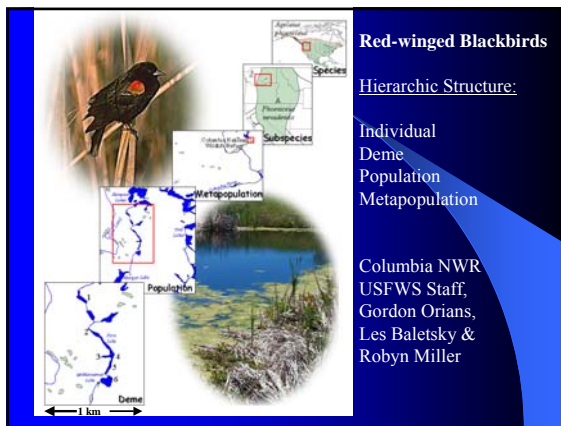
Hierarchically Structured Units: Biological

- Individual
- Deme
- Population (biological)
- Metapopulation

Deme

- "A group of individuals where breeding is random" (Emlen 1984).
- "A panmictic population" (Ehrlich and Holm 1963)

- Identification of demes and other groupings of individuals should be based on demography, movement, genetics and geography.

Deme

- Genetics: Random breeding within constraints of social system.
- Demography: Smallest grouping where its feasible to estimate birth, death, immigration and emigration rates.
- Movement: Restricted to home ranges in key seasons.
- Geography: Continuous distribution of individuals (one "patch" of habitat).

Population

- = a collection of demes with strong connections between adjacent demes

Population

- Demography: Very high correlations between demes.
- Movement: High rates of dispersal between adjacent demes.
- Genetics: Very closely related genetically.
- Geography: A collection of patches of habitat without great expanses of non-habitat intervening between them.

Metapopulation

- = " a population of populations" (Levins 1969)

Metapopulation

- Movement: Probability of dispersal between populations low but colonization occurs.
- Demography: Possible low correlations in rates produces high independence.
- Genetics: Genetic differentiation occurs between populations through time.
- Geography: Substantial areas of non-habitat may separate populations.

Metapopulation structure

Highly connected — Patch isolation — Highly isolated

Patchy
Classical
Mainland-island or Source-sink
Nonequilibrium

Occupied habitat patches
Vacant habitat patches
Boundaries of populations
Dispersal
Boundary of metapopulation

All small — Small and large — All large
Patch size (Based on Harrison and Taylor 1997; Stith et al. 1996)

Columbia NWR
USFWS Staff,
Gordon Orians,
Les Baletsky &
Robyn Miller

Metapopulation of Elk in Idaho

- Similarity or dissimilarity among populations from different locations based on genetic markers
- Population structure
- Demographic patterns

Photo: Hugh Hogle
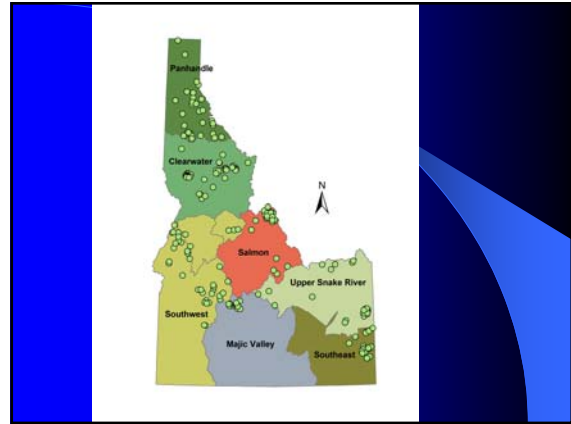
Percent of Individuals Correctly Assigned to Region

42.6%

Chesnimnus
44.4%

36.8%

27.8%
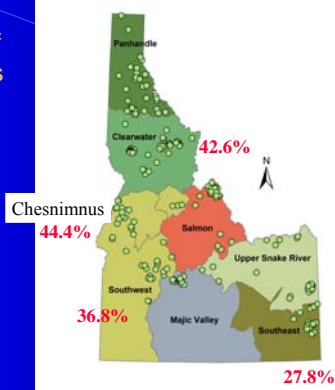
Significant Pairwise F_{st} Values

0.025

0.023

0.023

Washington

Calves: 100 Cows '87-'98

Panhandle

>34

Clearwater
<26

Chesnimnus

McCall
<26

Salmon
>34

Northern YNP

Teton Jackson Hole

Southwest
>34

Magic Valley

Southeast
>34

Oregon

Idaho

Wyoming

>34

>34
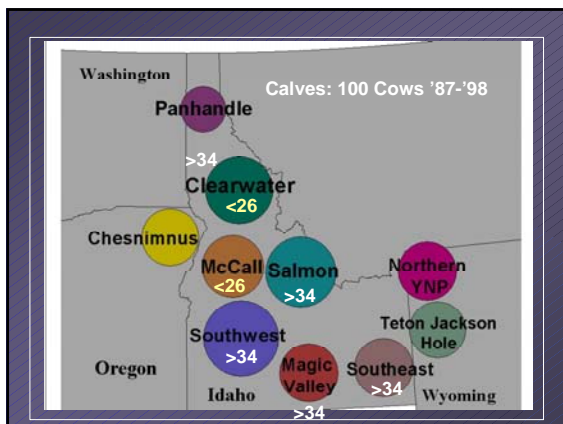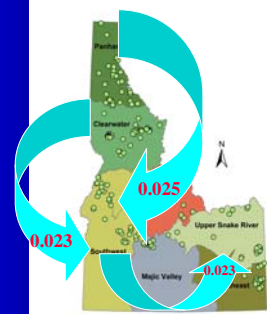
Elk Population Continuum

- Elk populations in the Northern Rocky Mountains
  - appear to be continuous
  - sufficient interchange of individuals occurs to limit genetic differentiation
  - Polziehn et al. (2000) found a similar pattern among 6 populations in the Canadian Rockies
  ** demographic patterns show more differentiation between populations

Greater Sage Grouse Metapopulation Genetic Differentiation

Sage-grouse Management Zones
Populations
Subpopulations
Leks
State / Province Boundaries

MZ I - Great Plains MZ | MZ III - Southern Great Basin MZ | MZ VI - Columbia Basin MZ
MZ II - Wyoming Basins MZ | MZ IV - Snake River Plain MZ | MZ VII - Colorado Plateau MZ
| MZ V - Northern Great Basin MZ |
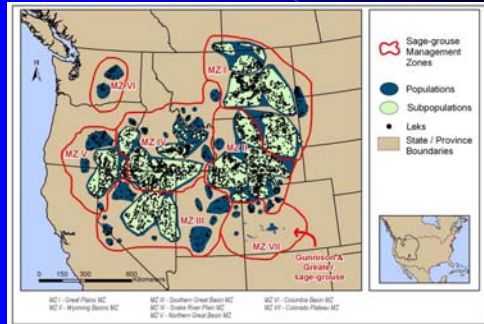
Selecting A Population Model

GMZ =	I	II	III	IV	V	VI	VII
Nmin(2007)	14814	42429	6851	15761	6925	315	241
SE	609	1467	435	676	464	59	52
CV (%)	4.1	3.5	6.3	4.3	6.7	18.7	21.5
Nmin(1965)	33287	92086	6461	52094	37915	1439[b]	255[c]
Years of data	43	43	43	43	43	41 [b]	24 [c]
Delta AICc for 4 models:							
EGPE [d]	1.4749	0	0	0	2.4109	2.4724	3.4264
Ricker	0.1835	0.6467	0.0194	1.3705	1.0706	0.3769	0
Gompertz	0	0.628	0.0919	1.1739	0	0	0.5621

PVA for GMZ 4 Population

- Exponential Growth Model with Process Error:
- Probability of extinction in 30 years
- depending on Extinction Threshold in Thousands
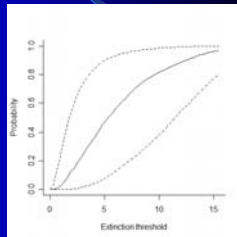
PVA for GMZ 4 Population

- Exponential Growth Model with Process Error:
- Probability of extinction in 100 years
- depending on Extinction Threshold in Thousands
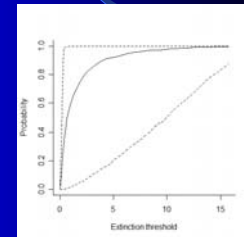
Sensitivity Analysis for GMZ 4 Population

- Exponential Growth Model with Process Error:
- Probability of extinction in 100 years
- Sensitivity to changes in a (mean rate of change), sigma, and ia (initial abundance)

PVA for GMZ 4 Population

- Gompertz Model :
- Probability of extinction in 100 years
- depending on Extinction Threshold in Thousands
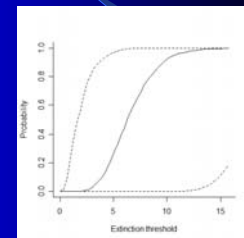
PVA for GMZ 4 Population

- Gompertz Model :
- Probability of extinction in 100 years
- depending on Extinction Threshold in Thousands
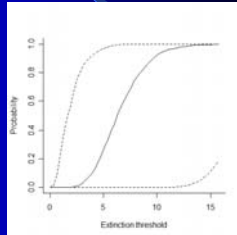
Sensitivity Analysis for GMZ 4 Population

- Gompertz Model :
- Probability of extinction in 100 years
- Sensitivity to changes in a (max rate of change), b (slope) sigma, and ia (initial abundance)
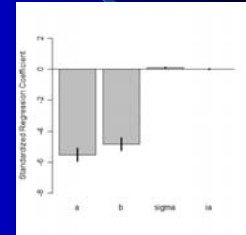
PVA for Washington Population

- Exponential Growth Model with Process Error:
- Probability of extinction in 30 years
- depending on Extinction Threshold in Thousands

PVA for Washington Population

- Exponential Growth Model with Process Error:
- Probability of extinction in 100 years
- depending on Extinction Threshold in Thousands
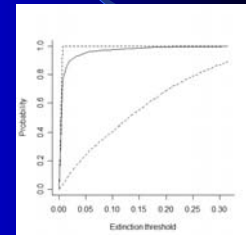
PVA for GMZ 6 Population

- Gompertz Model :
- Probability of extinction in 30 years
- depending on Extinction Threshold in Thousands
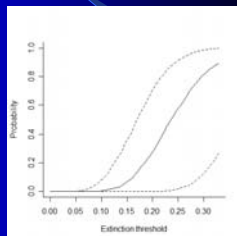
PVA for GMZ 6 Population

- Gompertz Model :
- Probability of extinction in 100 years
- depending on Extinction Threshold in Thousands
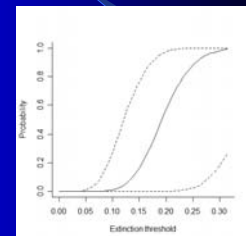
Demographic Correlations (SE) Among Sage Grouse Populations

	GMZ1	GMZ2	GMZ3	GMZ4	GMZ5	MZ6	GMZ7
GMZ1		0.481	0.190	0.303	0.041	0.279	-0.239
GMZ2	(0.138)		0.391	0.370	0.108	0.053	-0.168
GMZ3	(0.155)	(0.145)		0.651	0.514	0.204	-0.016
GMZ4	(0.150)	(0.146)	(0.120)		0.449	0.170	0.129
GMZ5	(0.157)	(0.157)	(0.136)	(0.141)		0.433	0.442
GMZ6	(0.151)	(0.158)	(0.155)	(0.156)	(0.142)		-0.327
GMZ7	(0.153)	(0.156)	(0.158)	(0.157)	(0.142)	(0.149)	

Dispersal Rates (SE) Among Sage Grouse Populations

	GMZ1	GMZ2	GMZ3	GMZ4	GMZ5	MZ6	GMZ7
GMZ1		0.050	0	0	0	0	0
GMZ2	(0.007)		0.020	0.011	0	0	0.009
GMZ3	0	(0.005)		0.024	0.004	0	0.005
GMZ4	0	(0.004)	(0.005)		0.035	0	0
GMZ5	0	0	(0.002)	(0.006)		0	0
GMZ6	0	0	0	0	0		0
GMZ7	0	(0.003)	(0.003)	0	0	0	

PVA for Metapopulation

- Exponential Growth Model with Process Error:
- Probability of extinction in 30 years
- depending on Extinction Threshold in Thousands
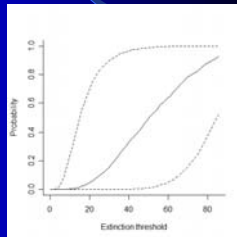
PVA for Metapopulation

- Exponential Growth Model with Process Error:
- Probability of extinction in 100 years
- depending on Extinction Threshold in Thousands
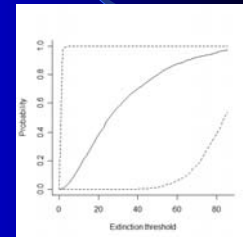
Sensitivity Analysis for Sage Grouse Metapopulation

- Exponential Growth Model with Process Error:
- Probability of extinction in 100 years
- Sensitivity to changes in a (mean rate of change), sigma, and ia (initial abundance)
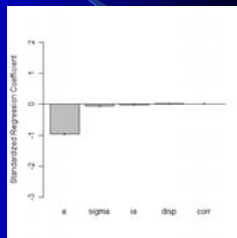
Questions?

Note literature cited

Gene flow: F_{st} measures how much of total variation (heterozygosity) is partitioned into sub-populations.

Washington
Panhandle
0.05
Montana
Clearwater
0.06
Chesnimnus
McCall Salmon
Northern
YNP
Teton Jackson
Hole
Southwest
Oregon
Magic
Valley
Southeast
0.05
Idaho
Wyoming
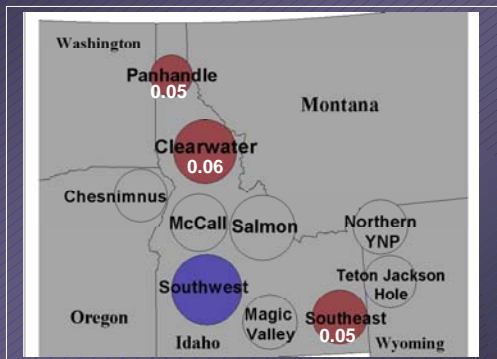
Hierarchy of Biological Populations, Spatial Units and Methods

Biological Unit	Spatial Unit	Method
Metapopulation	Region	Density
Population	Landscape	Survival, Fecundity
Deme	Interconnected Patches	Immigration, Emigration
Individual	Patch (fine-grained)	Home Range

Population Characteristics, Processes and Environment

Population Processes:
Birth
Death
Immigration
Emigration

Population Characteristics:
Abundance
Density
Sex Ratio
Age Distribution
Gene Frequency
Physiological State
Distribution Pattern & Scale
Movement Pattern

Environment:
Food
Cover
Water Conditions
Nest/Den Sites
Competitors
Predators
Diseases
Weather
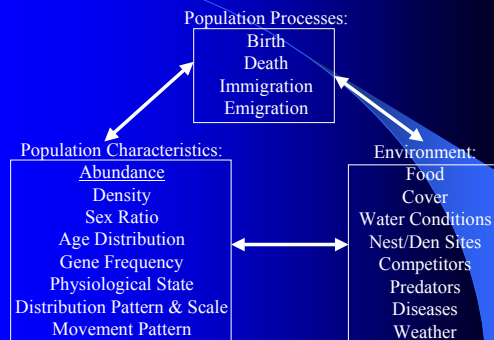
1) GUIDELINES FOR PRIORITIZING MANAGEMENT

- Provide guidelines for immediate actions to facilitate recovery and to direct adaptive management of T&E species with little existing data

- Target research needs for long-term management

GUIDELINES FOR PRIORITIZING MANAGEMENT

We aim to bridge the gulf between two paradigms:

Land manager intuition

- extensive local knowledge of system

- incorporates logistics and training constraints

Population models

- provide non-intuitive insights into mechanisms

Prioritizing management actions for species recovery

GUIDELINES FOR PRIORITIZING MANAGEMENT

We aim to bridge the gulf between two paradigms:

Land manager intuition

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Population models

- provide non-intuitive insights into mechanisms

Prioritizing management actions for species recovery

GUIDELINES FOR PRIORITIZING MANAGEMENT

SERDP · USGS *science for a changing world*

We combine these approaches to guide species management and prioritize data collection efforts for maximum efficacy

1) Developed models for species for which extensive data exists

2) Collected and analyzed data on which life-stages typical management actions can affect and by how much

---

MODELING APPROACH

SERDP *Strategic Environmental Research and Development Program* · USGS *science for a changing world*

Developed matrix models using species for which we do have extensive demographic data

Adult survival → Probability of breeding / Fecundity → Egg survival → Nestling survival → Age at maturation → Juvenile survival

---

MODELING APPROACH

SERDP *Strategic Environmental Research and Development Program* · USGS *science for a changing world*

$$
\begin{bmatrix} N_0(t+1) \\ N_{J_1}(t+1) \\ N_{J_2}(t+1) \\ N_{J_3}(t+1) \\ N_{J_4}(t+1) \\ N_A(t+1) \end{bmatrix} =
\begin{bmatrix}
0 & 0 & 0 & 0 & (B_S S_E S_0)0.5 & (B_A S_E S_0)0.5 \\
S_J & & & & & \\
& S_J & & & & \\
& & S_J & & & \\
& & & S_J & & \\
& & & & S_J & S_A
\end{bmatrix}
\begin{bmatrix} N_0(t) \\ N_{J_1}(t) \\ N_{J_2}(t) \\ N_{J_3}(t) \\ N_{J_4}(t) \\ N_A(t) \end{bmatrix}
$$

B_S = Annual probability an sub-adult breeds

B_A = Annual probability an adult breeds

S_E= Egg survival S_0 = Nestling survival

S_J = Annual juvenile survival S_A = Annual adult survival

MODELING APPROACH

Long-lived seabird: Hawaiian Dark-Rumped Petrel

Pohakuloa Training Area, Hawaii

Nest Success

Annual Adult Survival

Population increasing

Survival too low

Population decreasing

MODELING APPROACH

Long-lived seabird: Hawaiian Dark-Rumped Petrel

Pohakuloa Training Area, Hawaii

Nest Success

Annual Adult Survival

Population increasing

Nest success too low

Population decreasing

MODELING APPROACH

Long-lived seabird: Hawaiian Dark-Rumped Petrel

Pohakuloa Training Area, Hawaii

Nest Success

Annual Adult Survival

Population increasing

Which rates can change and by how much?

Population decreasing

PRIORITIZING MANAGEMENT

SERDP — Strategic Environmental Research and Development Program

USGS — science for a changing world

Not all aspects of a species' life history are created equal in their influence on overall population growth rate

To effectively manage species we need to know:

• Which rates can be affected through management actions, and the magnitude by which they can be altered

• What is the ultimate effect of different management actions on population growth rates

---

PRIORITIZING MANAGEMENT

SERDP — Strategic Environmental Research and Development Program

USGS — science for a changing world

Which rates are changed by management, and by how much?

Extensive literature search:
- contaminant removal, controlled burns, grazing/mowing, predator removal, brood parasite removal

- amphibians, birds, mammals and reptiles, plants

- criteria: studies must contain vital rates data from both **managed** and **unmanaged** populations (e.g. BACI or control treatment designs)

Meta-analytical approach to evaluate mean effects and patterns of variation

---

RESULTS

SERDP — Strategic Environmental Research and Development Program

USGS — science for a changing world

Example: studies of bird nest success
1) All management actions not created equal
2) Large variation across species

Y-axis: Proportional increase in bird nest success (0.8 to 1.8)

X-axis categories: Habitat alteration: controlled burn | Contaminant removal | Habitat alteration: grazing | Predator removal

SERDP
Strategic Environmental Research
and Development Program

RESULTS

USGS
science for a changing world

Meta-analysis results across studies

Nest success with predator removal program (y-axis)
Nest success with predators present (x-axis)

1) **mean 41% increase in nest success**

2) **significant heterogeneity of effect size between species**

SERDP
Strategic Environmental Research
and Development Program

RESULTS

USGS
science for a changing world

Nest success with predator removal program (y-axis)
Nest success with predators present (x-axis)

Predator removal programs appear to benefit tree nesting species more (P < 0.001)

SERDP
Strategic Environmental Research
and Development Program

RESULTS

USGS
science for a changing world

Hawaiian Dark-Rumped Petrel

Pohakuloa Training Area, Hawaii

Population increasing

Predator control?

Population decreasing

Nest Success (y-axis)
Annual Adult Survival (x-axis)
0.75 0.80 0.85 0.90 0.95 1.00

RESULTS

USGS
science for a changing world

Hawaiian Dark-Rumped Petrel

Pohakuloa Training Area, Hawaii

Reduce collision risk?

- **Light dimming**
- **Increased power line visibility**

Population increasing

Population decreasing

Nest Success — Annual Adult Survival

SERDP

RESULTS

USGS

Hawaiian Dark-Rumped Petrel

Pohakuloa Training Area, Hawaii

Population increasing

Population decreasing

Nest Success — Annual Adult Survival

SERDP

RESULTS

USGS

Trillium sp.:
Trillium reliquum

Fort Benning, Georgia

Recruitment (Germination) — Annual Survival of Reproductive Plants

RESULTS

Trillium sp.:
Trillium reliquum

**Fort Benning,
Georgia**

*Population
increasing*

*Population
decreasing*

Recruitment (Germination)

Annual Survival of Reproductive Plants

RESULTS

Trillium sp.:
Trillium reliquum

**Fort Benning,
Georgia**

*Population
increasing*

» **Decrease herbivory of
adult plants**

For *Trillium grandiflorium:*

*Population
decreasing*

Recruitment (Germination)

Annual Survival of Reproductive Plants

RESULTS

Trillium sp.:
Trillium reliquum

**Fort Benning,
Georgia**

*Population
increasing*

» **Decrease seed predation**

For *Trillium ovatum:*

*Population
decreasing*

Recruitment (Germination)

Annual Survival of Reproductive Plants

Elk demography: influence of vital rate variability

Elasticity (bar chart, y-axis 0 to 0.7): S_{calf}, S_{yr}, S_{cow}, S_{old}, S_{sen}, F_{yr}, F_{cow}, F_{old}, F_{sen}

Adult survival is 3-4 times more important to population growth than calf survival.

Bighorn sheep at Ram Mtn, Alberta, 1975-1995

Calf survival is up to 10 times more variable than adult survival.

Survival probability / Population size vs Year (75–95)
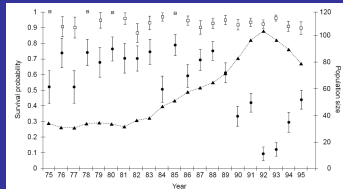
from Gaillard et al. 1998

The influence of vital rate variability in N. American elk

1. Collected vital rate estimates from across the range ($\approx$ 13 sites, $\approx$ 40 estimates)

2. Removed sampling variance

3. Used overall mean and variance in Life-Stage Simulation Analysis (LSA)

Life-stage diagram: 0 → 1 → 2 → 3 → 4 → 5 with S_{ca}, S_{yr}, S_{pa}, S_o, S_s and F_{yr}, F_{pa}, F_{oa}, F_{sa}

Calves, Yearlings, Prime-age adult (2-10), Old-age adult (11-15), Senescent adult (15+)
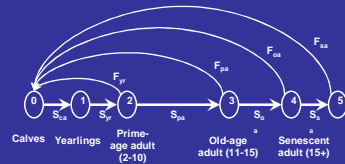
Constant adult survival, variable calf survival

Cow Survival (Cow survival estimate, 0.00–1.00)

Calf Survival (Calf survival estimate, 0.00–1.00)
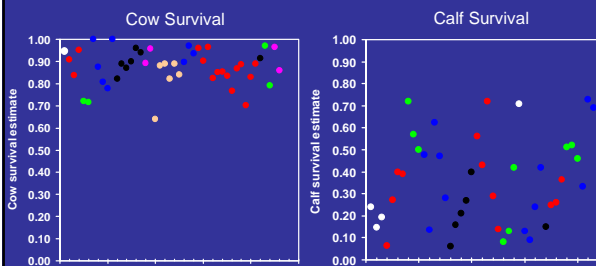
~ Process variance = 0.003 (53%)   ~ Process variance = 0.04 (89%)
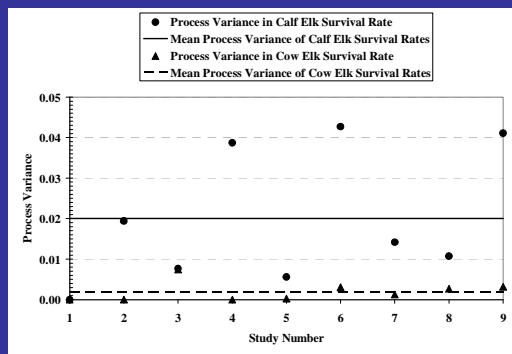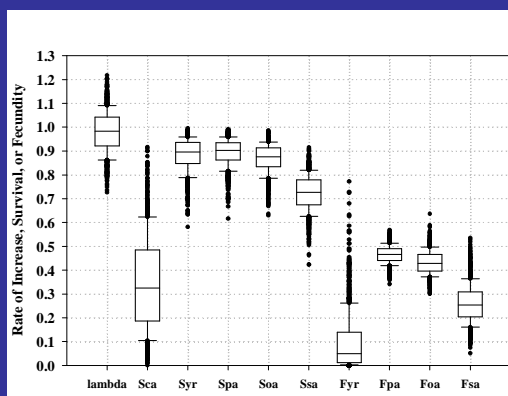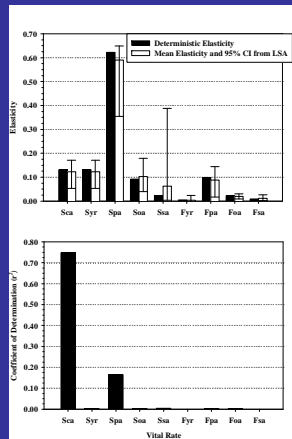
The importance of calf survival for elk populations
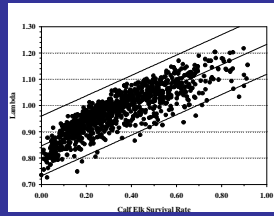
r² for calves = 0.75
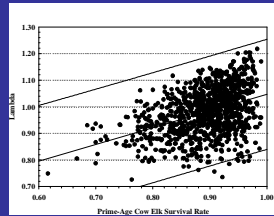
r² for adults = 0.16

Raithel, Kauffman & Pletscher, *in review*, JWM
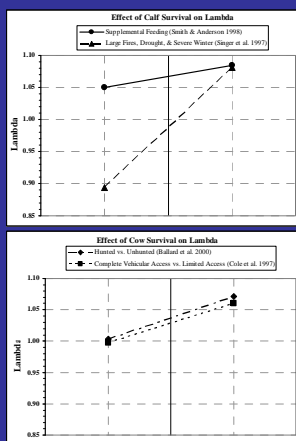
Amphibian declines and sensitivity analysis:
Identifying key life-history stages

Spotted frog (*Rana pretiosa*), Photo by Frank E. (Ed) Ely

(Biek, R., W. C Funk, B. A. Maxell, and L. S Mills. 2002. Conservation Biology)

Global amphibian declines

• Population declines and species losses

• Human-disturbed and "pristine"habitats

• Some causes identified: e.g. UV-B, habitat loss, fungal pathogens...

Examples

California tiger salamander
(*Ambystoma californiense*), Photo by
Gerald and Buff Corsi

Mountain yellow-legged frog (*Rana
muscosa*), Photo by Vance Vredenburg

Golden toad (*Bufo periglenes*)

Approaches currently used to understand amphibian declines

1. Monitoring

Population size

Time
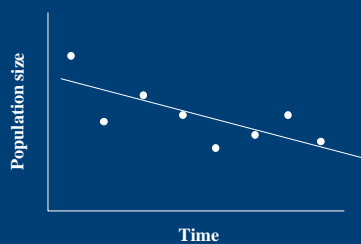
Approaches currently used to understand amphibian declines

2. Experimental studies
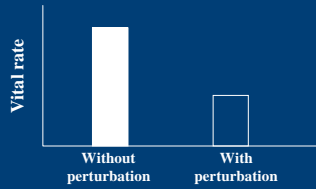
What is missing from amphibian decline research

Link between vital rate reductions and expected population-level responses

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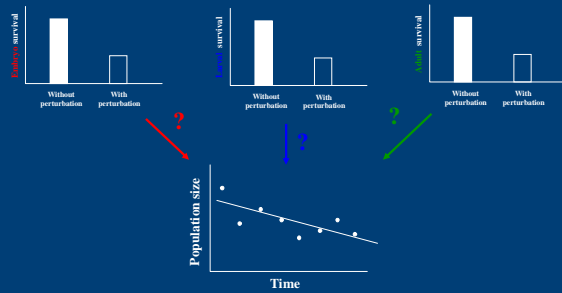
Objectives

Demonstrate how ecological sensitivity analysis can be used to:

1. Establish a link between vital rates and population level responses

2. Guide research and management priorities

Sensitivity analysis and amphibian declines

• Conducted elasticity analysis *and* LSA for three species:

Common frog (*Rana temporaria*), Photo by Eugene Bruins
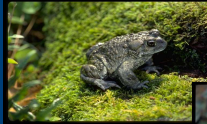
Western toad (*Bufo boreas*), Photo by Gerald and Buff Corsi

Red-legged frog (*Rana aurora*), Photo by Dong Lin

These species chosen because:

• Documentation of vital rates relatively thorough

• Local or regional population declines reported

• Mechanisms that reduced one or more vital rates identified

Life history pattern

F1

Prejuvenile G1 Juvenile G2 Adult

P1   P2

Prejuvenile = Embryo
+ Tadpole
+ Metamorph
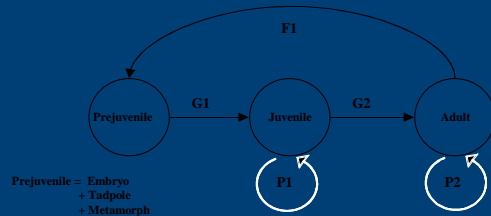
LSA results and interpretation

Main result
r² values differ substantially from elasticities and among species

Interpretation
• r² values weighted by vital rate variation
• vital rates with highest elasticities tend to have low levels of variation and, therefore, low r² values

Example: Western toad

r^2

S (adult)
S (embryo)

Elasticities

S (adult)
S (embryo)
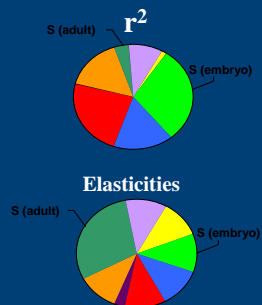
Management value of r²

Eliminating the lower range of variation of vital rates with high r² values is a good way to increase λ

λ

High r²

Normal range of λ

Higher range of λ

Vital rate

Decreased variation

Normal variation
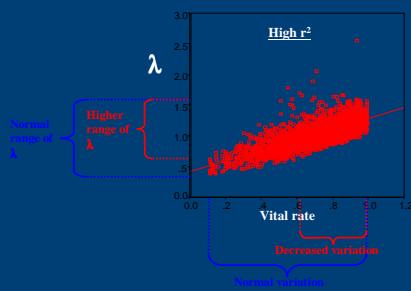
Utility of ecological sensitivity analysis for understanding, preventing, and reversing amphibian population declines

Elasticity analysis
• If any rate could be changed by the same amount, which will modify λ the most.

LSA
• Given that different rates can change by different amounts, identifies which changes most efficiently modify λ.

Policy implications for amphibian decline research

• Current emphasis on monitoring programs and experimental studies

• These approaches important, but equally important are
  basic population ecology studies to:
  1. Estimate vital rates (particularly lacking for amphibians)
  2. Understand population dynamics
  3. Predict population level effects of perturbations using
     modeling approaches such as sensitivity analysis

• Important to fund basic amphibian population ecology studies as
  well as monitoring programs and experimental studies

Mountain Mist Frog (*Litoria nyakalensis*),
Photo by J-M. Hero

Predicting effects of wolf reintroductions on ungulate populations: Comparing model predictions to observations for elk and wolves in Yellowstone.

– by Edward O. Garton[1], Douglas W. Smith[2], Bob Crabtree[1], Bruce Ackerman[1], and Gerry Wright[1]

– 1. Fish and Wildlife Dept., University of Idaho, Moscow, ID 83844,

– 2. National Park Service, Yellowstone Center for Resources, P.O. Box 168, Yellowstone National Park, WY 82190

Overview

- Can we correctly estimate effects of reintroduced wolves?
- Modelling project for National Park Service in 1990 to answer key questions before wolves were reintroduced to Yellowstone
- Assess success of the predictions
- Implications for management today

The Question in 1990: What would be the impact on the Northern Yellowstone elk herd of a wolf reintroduction to Yellowstone National Park?

- My research group and Mark Boyce (Univ. Wyoming) were each invited separately to take a modeling approach to answer this question.

1990 Approach

- Evaluate dynamics of Northern Yellowstone Elk Herd using available data
- Predict characteristics of wolf population growth and predation from literature
- Build an empirically based projection model
- Validate portions of the model by comparing predictions to observed data in 1990

Requirements in 1990

- Deterministic, mechanistic model [Simple, clear]
- All parameters (values) based on peer-reviewed scientific literature or our own estimates:
- Northern Yellowstone elk herd (Houston 1982)
  - Ungulate ecology
- Wolf population dynamics (Mech 1970)
- Wolf predation on
  - Moose
  - Deer
  - Elk (Carbyn 1974, 1983, Weaver 1979)

Results

- Garton, E.O., R.L. Crabtree, B.B. Ackerman, and and G. Wright. 1990.
- The potential impact of a reintroduced wolf population on the northern Yellowstone elk herd. Pages 3-59 to 3-91 in
- Wolves for Yellowstone? A report to the United States Congress. Vol. II: Research and and analysis. National Park Service. Yellowstone Yellowstone National Park. 571 pp.

Results

- Singer, F.J., W. Schreier, J. Oppenheim, and E.O. E.O. Garton. 1989.
- Drought, fires and large mammals.
- *Bioscience* 39:716-722.

Model Format and Input Parameters

- ELK HAVE 21 AGE CLASSES AND 5 AGE GROUPS
- STARTING   GROUP
-    AGE   NAME
-    0   CALF
-    1   YEARLING
-    2   2-YR_OLD
-    3   PRIME
-    9   OLD

FECUNDITY REGRESSION COEFFICIENTS
(CONSTANT, POPULATION SIZE, WINTER SEVERITY)
FOR EACH OF THE 5 AGE GROUPS ARE:

AGE GROUP		CONSTANT	POPN-SIZE	WINTER SEVERITY
1	CALF	0.0	0.0	0.0
2	YEARLING	0.5512	-0.0000273	0.1485
3	2-YR_OLD	1.5023	-0.0000257	0.0377
4	PRIME	1.596	-0.00003130	0.04006
5	OLD	0.982	0.0	0.0

SURVIVAL REGRESSION COEFFICIENTS
FOR MALES

AGE GROUP	CONSTANT	POPN-SIZE	WINTER-SEVERITY
CALF	-12.753	0.00284	-2.12
YEARLING	-3.177	0.00168	-1.34
2-YR_OLD	-3.177	0.00168	-1.34
PRIME	-3.177	0.00168	-1.34
OLD	-3.177	0.00168	-1.34

SURVIVAL REGRESSION COEFFICIENTS

FOR FEMALES

AGE GROUP	CONSTANT	POPN-SIZE	WINTER-SEVERITY
CALF	-12.753	0.00284	-2.12
YEARLING	-9.179	0.0014	-3.142
2-YR_OLD	-9.179	0.0014	-3.142
PRIME	-9.179	0.0014	-3.142
OLD	-9.179	0.0014	-3.142

VULNERABILITY TO HARVEST AND PREDATION

	WOLF		HUMAN	
	MALE	FEMALE	MALE	FEMALE
CALF	8.400	8.400	0.370	0.370
YEARLING	8.200	8.200	1.000	0.560
2-YR_OLD	2.500	2.500	1.000	0.560
PRIME	1.000	1.000	1.000	0.560
OLD	6.500	6.500	1.000	0.560

Key Questions: Elk Population Dynamics

- Number of elk
  - Visibility bias
- Annual Mortality
  - Density-dependent?
- Natural and Harvest Mortality
  - Additive or compensatory?

Annual Mortality Rate of Calves

MORTALITY RATE (PERCENT)

POPULATION SIZE (Thousands)

Observed — Predicted — Lower & Upper 95% CI

Annual Mortality Rate for Cows

MORTALITY RATE (PERCENT)

POPULATION SIZE (Thousands)

Observed — Predicted — Lower & Upper 95% CI

Annual Mortality Rate for Bulls

MORTALITY RATE (PERCENT)

POPULATION SIZE (Thousands)

Observed — Predicted — Lower & Upper 95% CI

Total Mortality and Harvest
Bulls

$r^2=64\%$

$r^2=67\%$

Best Model: Inverse density-dependence +
100% compensatory harvest mortality: $r^2 = 82\%$

MalTotM

MalHarv
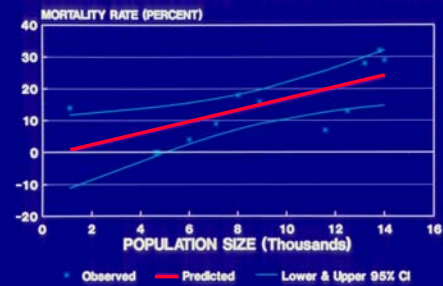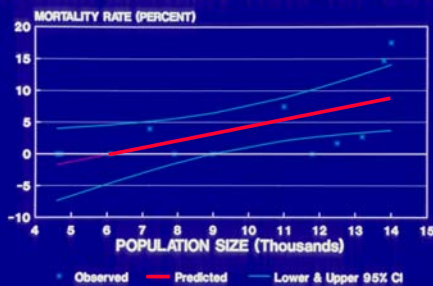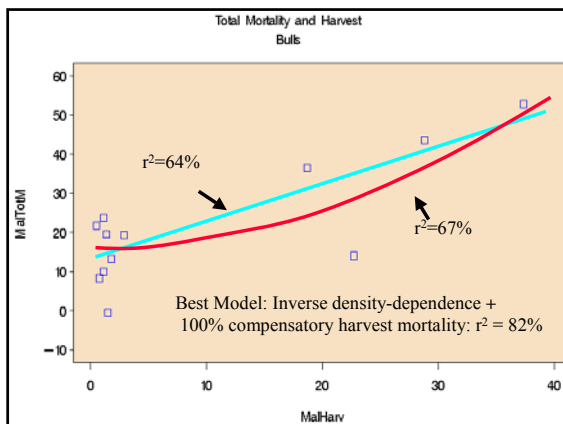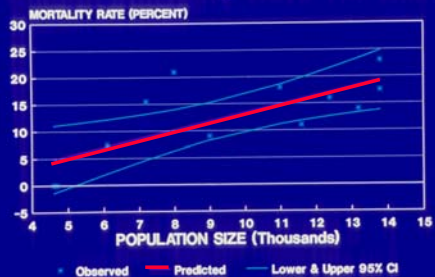
Total Mortality Rate and Harvest of Cows and Calves

- Models for cows:
  - Harvest is 88-96% additive
  - Best model incorporating density-dependence and winter severity implies that harvest is almost completely additive.
- Models for calves:
  - All models, including ones incorporating density-dependence, imply harvest is completely additive.

WOLF POPULATION DYNAMICS

AND PREDATION

- ▸ Recruitment
- ▸ Mortality
- ▸ Pack size
- ▸ Territory size

Wolf Pup Recruitment
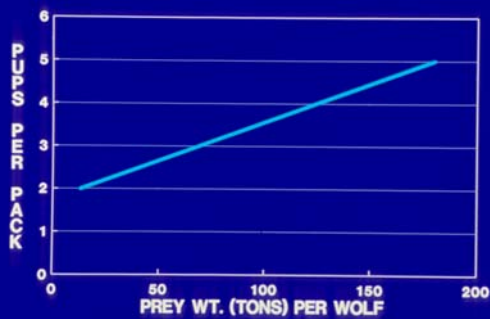
Wolf Survival Rates

Dispersal?

BETAS   ALPHAS
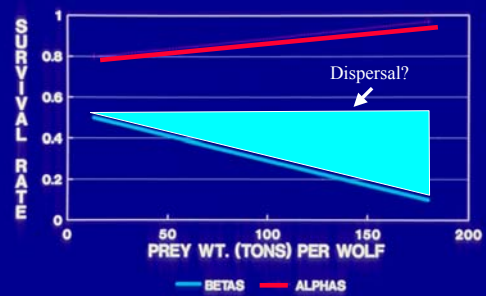
Wolf Numbers

- Territorial behavior of wolves
- Predict number of packs and pack size from prey biomass (tons available per wolf)

FUNCTIONAL RESPONSE

- ▸ Search Rate

- ▸ Handling Time
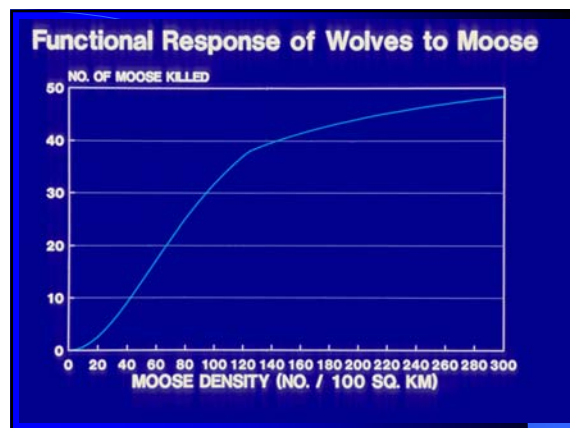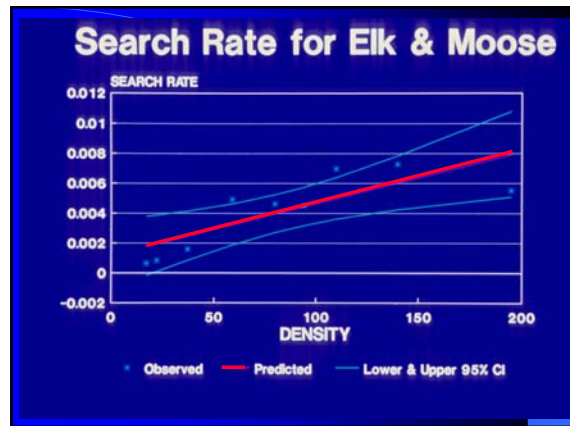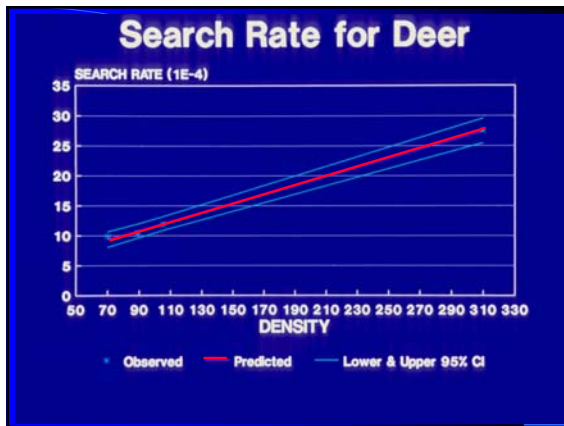
Search Rate for Deer

SEARCH RATE (1E-4)

DENSITY

Observed — Predicted — Lower & Upper 95% CI

Search Rate for Elk & Moose

SEARCH RATE

DENSITY

Observed — Predicted — Lower & Upper 95% CI

Handling Time for Moose

HANDLING TIME (DAYS)

PACK SIZE

Observed — Predicted — Lower & Upper 95% CI

Functional Response of Wolves to Moose

NO. OF MOOSE KILLED

MOOSE DENSITY (NO. / 100 SQ. KM)

VULNERABILITY TO HARVEST AND PREDATION

	WOLF		HUMAN	
	MALE	FEMALE	MALE	FEMALE
CALF	8.400	8.400	0.370	0.370
YEARLING	8.200	8.200	1.000	0.560
2-YR_OLD	2.500	2.500	1.000	0.560
PRIME	1.000	1.000	1.000	0.560
OLD	6.500	6.500	1.000	0.560

Projected Wolf Population

NUMBER OF WOLVES

YEAR

PUPS — TOTAL WOLVES

Yellowstone Elk Projections
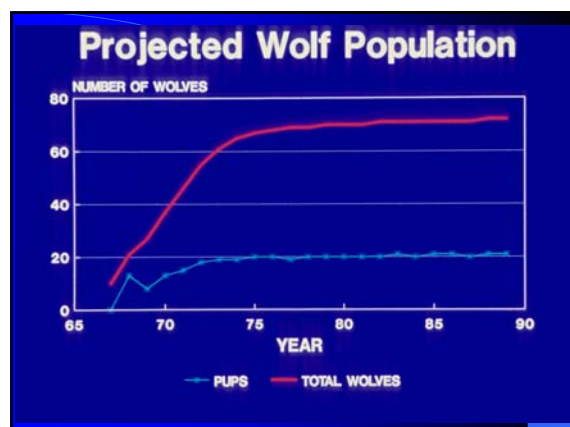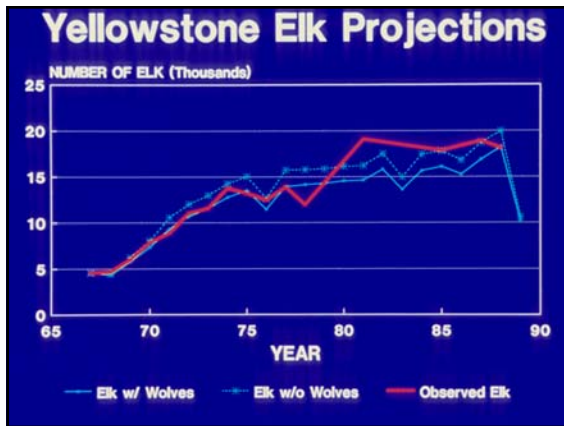
Comparing Model Predictions to What Happened 1995-2005

- Wolf population on the Northern Range increased from 21 at introduction (1995) to 69 by 2000
- Fluctuated from 58 to 98 since then with an average over last 7 years of 75.
- Confirms model predictions nicely!

Comparing Model Predictions to What Happened 1995-2005

- Elk population raw (uncorrected) counts have fluctuated between 8,300 and 14,500 with a generally downward trend.
- Model predicts stable population around 10,000 elk on Northern Range but sensitive to following:

Implications: Hunter Harvest
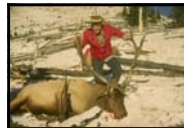
- Population trend for Northern Yellowstone Elk herd at current size is very sensitive to
- Human harvest rate:
- @ 9% harvest ('70-'80s) - Stable with wolves
- @ 11% harvest ('95-'05) - Declines with wolves
- @ 7% harvest - Increases with wolves
- @ 9% harvest - Increases without wolves

Implications: Winter Severity

- Population trend for Northern Yellowstone Elk herd at current size is very sensitive to winter severity:
  – Average severity: population stable
  – Mild winters: population increases 10% / year
  – Severe winters: population decreases 10% /year
- In 1/3 of years, population either increases or decreases at least 10%

Implications: Elk Productivity

- High wolf predation on older, menopausal cows shifts age structure of females to younger more fecund females.
- Increased average female productivity partially compensates for higher mortality rate of calves due to wolf predation and human harvest of male calves.

Implications: Persistence

- High probability of persistence of Northern Yellowstone elk herd in face of both wolf predation and hunter harvest on Northern Range because of strong inverse density-dependence of vital rates:
  - Female productivity
  - Survival of calves, cows and bulls

Conclusions

- 1990's predictions successful for wolves
- Northern Yellowstone elk herd projected to be stable with high chance of persistence but average abundance depends on
  - Hunter harvest
  - Winter severity

Stochastic Density-Dependent Elk Population Model

- Generalized elk-wolf model for Yellowstone to apply to other elk populations based on relative size and productivity of summer and winter ranges, pregnancy rates, etc.

Harvest in Blue Mountains

Spikes No.	Percent	Adults No.	Percent	Tot Bulls No.	Percent	Antlerless Total	Percent
278	66.67	78	23.01	356	47.09	281	7.07
190	67.62	82	25.47	272	45.11	243	7.91
241	68.47	64	15.31	305	39.61	167	4.92
177	68.34	64	17.25	241	38.25	15	0.46
138	61.61	69	22.77	207	39.28	109	3.41
309	77.64	71	28.63	380	58.82	57	1.95
107	46.93	41	15.02	148	29.54	61	1.84
169	64.75	40	13.99	209	38.21	28	0.84
Mean 201.13	65.25	63.63	20.18	264.75	41.99	120.13	3.55
SD 69.40	8.70	15.57	5.49	79.21	8.58	100.23	2.82

Projected Blue Mountain Elk

Line chart: Elk Population (y-axis, 0–6000) vs Year (x-axis, 1–19). Two series: Males and Females.
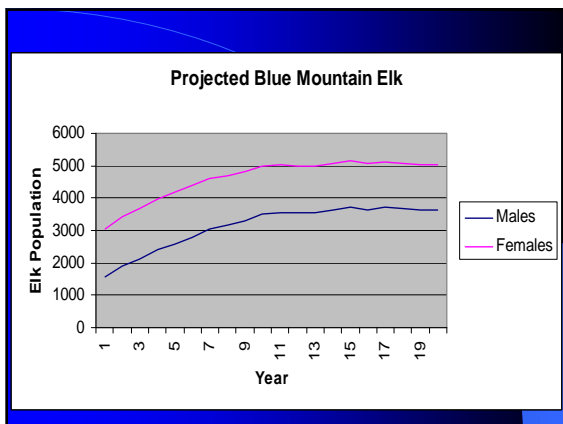
Stochastic Population Projections

- **Mean   SD**
- **450.0   0.0** Winter Range in square miles
- **1100.0   0.0** Summer Range in square miles
- **0.0   1.0** Winter Severity
- **0.79   0.087** Spike Harvest as a proportion of spikes in fall
- **0.24   0.055** Adult Bull Harvest as a prop. of fall adult bulls
- **0.043   0.028** Antlerless Harvest as a proportion of fall cows + calves

Stochastic Projections

Distribution of Population Abundances

Questions?

POTENTIAL IMPACT OF WOLVES ON THE NORTHERN YELLOWSTONE ELK HERD

E. O. Garton
B. Crabtree
B. Ackerman
G. Wright
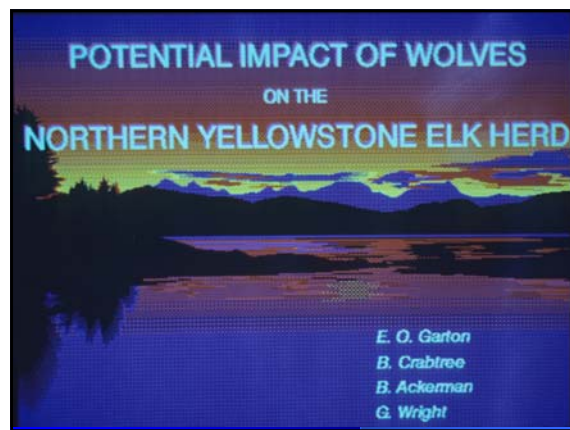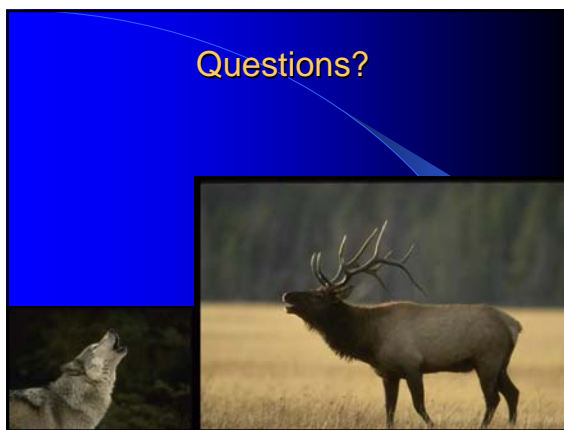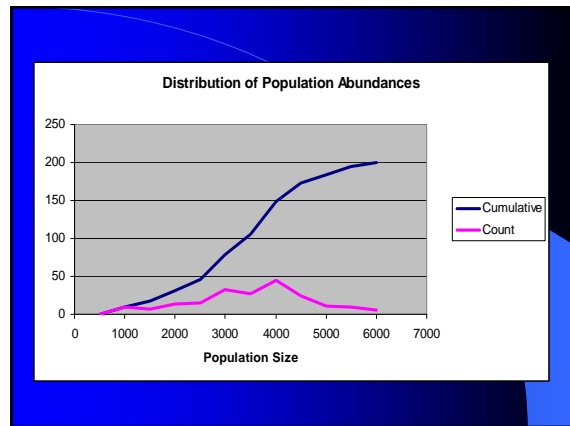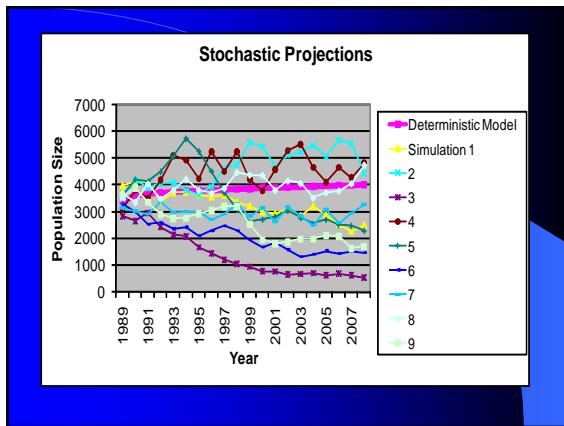
Metapopulation viability of the golden-cheeked warbler: issues and potential of a global sensitivity analyses

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Strategic Environmental Research and Development Program

University of Idaho

USGS
science for a changing world

Golden-Cheeked Warbler
(*Dendroica chrysoparia*)

- breeds in closed-canopy woodlands, primarily Ashe juniper and oak
- declined due to habitat loss and fragmentation from clearing of juniper for urban expansion, agriculture, and commercial harvest

---

Golden-Cheeked Warbler Recovery

- Habitat protection
  - reserve systems should include habitat most likely to contribute to recovery
- Conservation incentive programs
  - provide financial support to landowners for protecting habitat
  - sell "credits" to developers seeking mitigation

- Need objective, quantitative methods for assigning recovery value to habitat patches

Valuing Habitat for GCWA Recovery

- All habitat patches are not created equal

- Multiple population (metapopulations) models must consider characteristics that vary among and within populations

- Objective: Evaluate important drivers of metapopulation viability

---

Multiple Population Models

- Inputs
  - Demographics (stage/age-specific)
    - Survival
    - Reproduction
  - Population parameters
    - Number of populations (habitat patches)
    - Initial abundance
    - Size of habitat patch (K)
  - Metapopulation dynamics
    - Dispersal among habitat patches
    - Correlated demographics among patches

- Output
  - Metapopulation viability (e.g., probability of persistence)

Multiple Population Models

- How can we evaluate how changes in the inputs (e.g., management actions across space) relate to changes in output (i.e., metapopulation viability), in the face of uncertainty?

- Very complex model
  - Large number of input parameters (e.g., 100s)
  - Management affects parameters differently
  - Non-linear response to changes
  - Interactions among input parameters

- Need: Methods and Software
  - Global Sensitivity Analysis of Metapopulation Viability Models

Global Sensitivity Analysis

Input Parameters

X1   X2   X3

...

Parameter Importance

X2: Survival of Population 2
X3: Size of Pop. 2 habitat
X1: Reproduction of Population 1
.
.
.

Viability model

$$y = f(X_1, X_2, X_3, ...)$$

Partitioning var(y)

X1
...
X2
X3

Output distribution

var(y)

Sensitivity Analysis Method
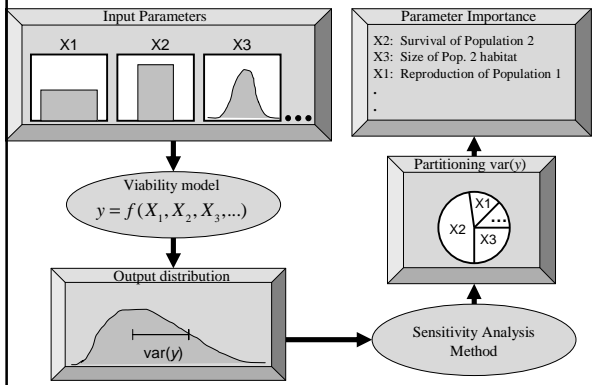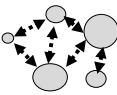
The Software

- Developed software (MetaPVA)

Metapopulation Viability Analysis

Status			Parameters
completed	**Step 1:**	Enter/Edit Simulation Setup	Number of replications, Number of time steps, Extinction threshold, Demographic stochasticity option
completed	**Step 2:**	Enter/Edit Species Data	Number of stages, Leslie stage matrices, Metapopulation-level density dependence, Stage-specific dispersal
complete	**Step 3:**	Enter/Edit Population-specific Data	Initial abundances, Density dependence type and parameters, Population-specific relative fecundity and survival, Stage matrix selection
not completed*	**Step 4:**	Enter/Edit Metapopulation Data	Correlations among populations, Dispersal among populations

* Note: Step 4 does not have to be completed to run simulations

Run This Scenario   Save Output   Sensitivity Analysis

What patch and population characteristics are most important to GCWA metapopulation viability?

The Model

- Stochastic, demographic-based, metapopulation projection model (e.g., RAMAS MetaPop)*
- Stage matrix

- Ceiling carrying capacity (K)
- Symmetric dispersal (14%)

Fort Hood

Balcones NWR

* Alldredge et al. (2004)

Sensitivity Analysis

- Sensitivity parameters: Survival, reproduction, K, dispersal

- Input values: Uniform distributions +/- 10% of nominal values

- Output metric: mean final population size after 20 years (100 replications)

- Linear regression: standardized regression coefficients

Results
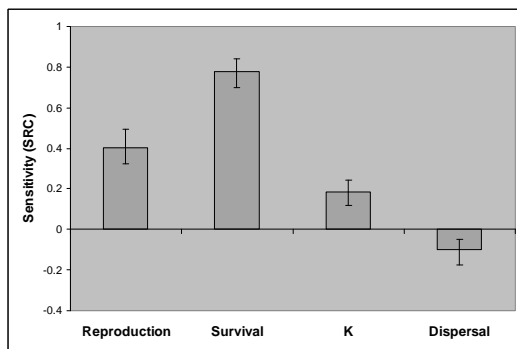
Sensitivity to Individual Populations

- What about the importance of individual populations?

Smaller is better??

Balcones

Fort Hood
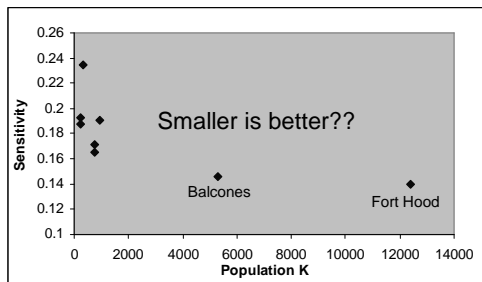
- Input values: Each population's K +/- 200

Population Trajectories (No dispersal)

Carrying Capacity (K)
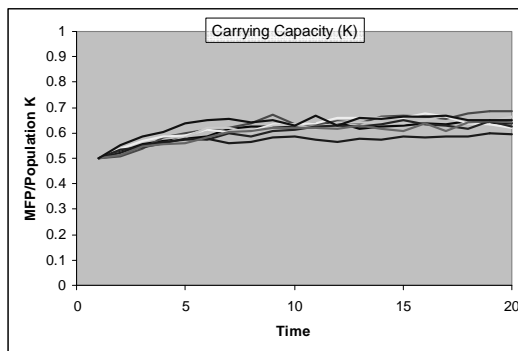
Population Trajectories (Dispersal = 14%)
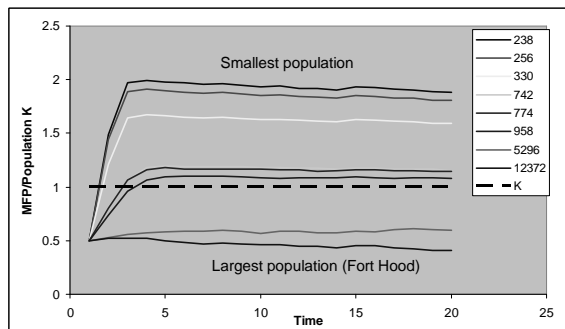
The Devil in the Details

• Model Assumes:
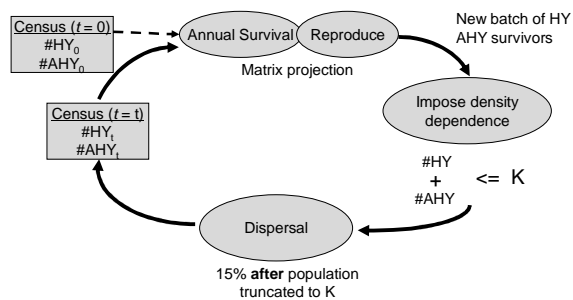
GCWA Life History
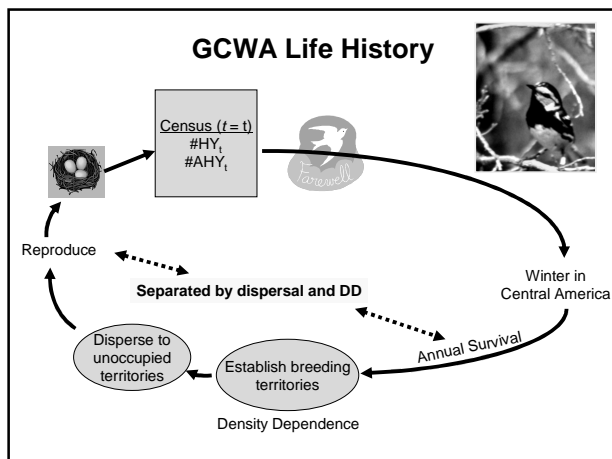
The Punchline

Our current simulation model

1. Survival
2. Reproduction
3. Density dependence
4. Dispersal

Our "new" simulation model

1. Survival
2. Density dependence
3. Dispersal
4. Reproduction

Lessons Learned

- "Garbage in, garbage out…"
- Model structure also matters
- Start with Life History Sketch
- If LHS doesn't match model structure in simulation program, BE CAUTIOUS!
- Sensitivity analysis helpful for identifying errors in model structure

Questions, comments, ideas?

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Conservation of Wildlife Populations

Demography, Genetics, and Management

L. Scott Mills

Dedication

For my father, who instilled in me a profound respect and appreciation for the natural world.

Contents

7

Accounting for age- and sex-specific differences: population-projection models

For what is man? First, a child, soft-boned, unable to support itself on its rubbery legs, befouled with its excrement, that howls and laughs by turns, cries for the moon but hushes when it gets its mother's teat; a sleeper, eater, guzzler, howler, laugher, idiot, and a chewer of its toe; a little tender thing all blubbered with its spit, a reacher into fires, a beloved fool.

Thomas Wolfe (1942:432), You Can't Go Home Again

If you can't generalize from data there's nothing else you can do with it either. A science without generalization is no science at all. Imagine someone telling Einstein, "You can't say 'E=mc².' It's too general, too reductionist. We just want the facts of physics, not all this high-flown theory. Cuckoo."

Robert Pirsig (1992), Lila

Introduction

Bull elk, cowbird eggs, frog larvae, mother wallabies, turtle hatchlings. Often wildlife ecologists care about particular parts of a population as much as they do the population as a whole. Whether the applied goal is to harvest, recover, reduce, or reintroduce wildlife populations, one cannot long avoid the dynamics of particular ages, stages, and sexes. The last two chapters have described a foundation for how to predict and describe changes in wildlife populations, but thus far dynamics have been described by a single term (λ or r) applied to the total population size (N). In this chapter I will explore how particular groups of individuals, and their birth and death rates, affect population growth and the likely numbers of individuals of different classes.

Here is a story to transition us, adding the wrinkles of age and sex structure (Coulson et al. 2001). Soay sheep studied on the island of Hirta, off the coast of Scotland, fluctuate dramatically, more than expected based on weather or density dependence alone. Why? In large part because survival of lambs and older males is heavily influenced by winter weather, whereas yearlings and prime-aged females are

most affected by rainfall at the end of winter. Meanwhile, negative density dependence affects lambs and older females more than prime-aged adults or yearlings. In turn, the changing proportions of different sex and age classes caused by weather and density dependence cascades into effects on population growth (see also Box 9.3). Not all sheep are equal (Gaillard et al. 2001). Counting the sheep as equivalent, ignoring age and sex, would tell us very little about how ecological stresses affect population fluctuations or population growth.

For humans and a few other species, age can be tracked as a meaningful descriptor of an individual. However, vital rates in wild populations often depend on developmental, morphological, or even behavioral stages more than calendar age. Consider, for example, larval forms and adults in amphibians, fish of different sizes, or big trees and saplings. Furthermore, different stages can often be distinguished more easily in the field than age classes can, and management often centers more on recognizable stages than on ages (e.g. ungulate males of different sizes or antler-development stages). The predominance of stage structure means that throughout this chapter (and the book), I will refer to **stage** instead of repeating age or stage.

In basic ecology classes, age or stage structure is typically covered using life tables. Although life tables are important for basic ecological understanding, most of the applied things that life tables can tell us about wildlife population dynamics (e.g. estimates of λ, stage structure, and reproductive value) can be better estimated using matrix-projection models[1]. Thus I will skip life tables and focus on less well known yet more versatile and practical tools for understanding how structure affects wildlife population dynamics.

Specifically, the aim of this chapter is to describe the wonders of matrix-projection models for understanding wildlife populations. If the thought of matrix math makes you nervous, think of a population-projection matrix as merely a box to help keep straight the bookkeeping of birth and survival, a mathematical representation of biological processes. That's it, really. Lots of bells and whistles can be added to matrix projections, but at their heart they are less intimidating than they may look. So let's look at what a matrix is, then we will quickly come back to the surface to gulp the air of application to wildlife population biology.

Anatomy of a population-projection matrix

Throughout the chapter, I will use as a tangible example the common frog, a species found throughout much of Europe. The projection matrix, **M**, is a square of k columns and k rows, where k is the total number of stage classes (Fig. 7.1). Each element (or cell) of the matrix contains a value that is used to project stage-specific reproduction or survival forward one time step. A time step can be anything:

---

[1] For good overviews linking life tables to matrix models, see Noon and Sauer (1992) and Case (2000).

diagonal of the matrix must be zero. For practical purposes the distinction between Leslie and Lefkovitch matrices is only important to help you understand the terms in published papers.

With this brief lesson in projection-matrix anatomy, a few biological generalizations should become clear. First, each element of the top row of the matrix represents the reproductive contribution of each stage to the next time step. Second, the survival of individuals of any stage to the next time step (e.g. annual survival) can be determined from any matrix by adding up all the values for that column, excepting the first row[2]. For example, for the frogs in Fig. 7.1, annual survival of juveniles would equal 0.33, the sum of the proportion of juveniles that survive and become juveniles (0.25) plus the proportion of juveniles that survive and become adults (0.08). Third, the rates in the matrix must correspond to the stages you are interested in projecting. In particular, where the sexes have different survival rates, or where reproduction is known for females only, the vital rates are often female-based. In other cases, male-based models are most appropriate, as you will see for the red-cockaded woodpeckers in case study 1, below; two-sex matrix models are also possible, and you will see an example for ungulates in Chapter 14. The important thing is to be clear about which sexes are included in the projection, and how.

How timing of sampling affects the matrix

Because we are discussing applied population biology, let's think more about how to link the model to the field data, particularly to observable stages and to the timing of the surveys that produced estimates of vital rates (Fig. 7.2). Because each element of the top row contains the reproductive contribution of class j to the first stage class in the next time step, the top-row elements contain not only stage-specific fecundity (m_j), but also a term to advance the newborns to the next time step[3]. What does that mean? Well, newborns have to survive to be counted, or mothers counted last year have to survive to successfully bear their babies next year. So reproduction to the next time step depends on two terms: fecundity (m) and survival (P).

Exactly what we put into the elements of the top row depends on the kind of data collected. Suppose we were interested in projecting population growth for American bison, a species where most young are born at nearly the same time. For simplicity, assume all calves are born on May 31, and consider only the female portion of the population. If

---

[2] When building a matrix from field-collected vital rates, one of many decisions is how to partition annual survival into the appropriate elements in a stage-based model. Crouse et al. (1987) give a nice, simple approach to partitioning survival into matrix elements for a stage-based model.

[3] Remember, fecundity (or m_j) refers to the average number of offspring an individual in stage j produces in a year (see Chapter 4); if you are familiar with life tables, then m_j is the same as the m_x or b_x. I use reproduction to next time step for the top-row matrix elements that include both the fecundity and survival terms needed to project the fecundity to the next time step; this is often called fertility by human demographers, but fertility has different meanings in the ecological literature so I will avoid the term here.

| | From this stage... | | |
To this stage...	Pre-juvenile	Juvenile	Adult
Pre-juvenile	0	52	279.5
Juvenile	0.024	0.25	0
Adult	0	0.08	0.43

Fig. 7.1 Anatomy of a female-based projection matrix, using as an example the common frog (Biek et al. 2002; see also Box 4.8). This species has three stages: pre-juvenile (first year, consisting of the embryo, tadpole, and overwintering metamorph), juvenile (next 2 years), and adult. The projection interval, or time step, for this matrix is 1 year. The first row represents reproduction from each stage to the next year. The diagonal (e.g. $a_{2,2}$=0.25 and $a_{3,3}$=0.43; see text for an explanation of this notation) represents the proportion of individuals in a stage that will survive and still be in the same stage next year, while the subdiagonal (just below the diagonal; e.g. $a_{2,1}$=0.024 and $a_{3,2}$=0.08) represents the proportion surviving and advancing to the next stage next year.

for a yeast, the relevant time step of life and death might be an hour; for small mammals, it might be a month. For logistical and biological reasons, however, the most common time step for wildlife studies is a year, so throughout the book I will often use the terms year or annual as shorthand for the more general time step.

The elements of a matrix are described with subscripts that tell what row and column they are in (with the row first and the column second); for example, element $a_{2,1}$ is the element in row 2 and column 1. A handy way to decipher the biological meaning of any matrix element is to label the rows and columns of the matrix with the consecutive stages of your organism. Each element gives the transition – one time step later – from whatever column the number is in to whatever row the number is in. Another way to say the same thing is that a_{ij} represents the number of individuals contributed on average by each individual in class j at the current time step to class i at the next time step. For the common frog in Fig. 7.1, element $a_{2,1}$ is 0.024, meaning that on average 0.024 (or 2.4%) of the pre-juvenile frogs in the population survive to become juveniles the next year.

Notice in Fig. 7.1 that animals can remain in some stages for multiple time steps (for example 0.25 of the juveniles can remain as juveniles and 0.43 of the adults as adults). In a stage-based matrix, otherwise known as a **Lefkovitch matrix** (Lefkovitch 1965), transitions from any stage to any other stage can be accommodated. Stage-based matrices are more versatile than the original **Leslie matrix** (Leslie 1945), whereby vital rates depend on ages that are identifiable, and where the span of each age is the same as the length of the time step. In a Leslie matrix, an individual can only survive and transition to the next age, or die, so everything below the first row and not on the sub-

(a)

Sampling happens just before birth pulse

Birth pulse   Survival to next year

Sample t Sample $t+1$

N_{zero}, N_1, N_2, N_3 — m_1, m_2, m_3, P_0, P_1, P_2, P_3

$$\begin{bmatrix} m_1P_0 & m_2P_0 & m_3P_0 \\ P_1 & 0 & 0 \\ 0 & P_2 & P_3 \end{bmatrix} * \begin{bmatrix} N_1 \\ N_2 \\ N_3 \end{bmatrix}$$

(b)

Sampling happens just after birth pulse

Sample t

Birth pulse   Survival to next year   Sample $t+1$

N_{zero}, N_1, N_2, N_3 — m_1, m_2, m_3, P_0, P_1, P_2, P_3

$$\begin{bmatrix} m_1P_0 & m_2P_1 & m_3P_2 & m_3P_3 \\ P_0 & 0 & 0 & 0 \\ 0 & P_1 & 0 & 0 \\ 0 & 0 & P_2 & P_3 \end{bmatrix} * \begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ N_3 \end{bmatrix}$$

Fig. 7.2 General schematics of the birth and death processes captured when the sampling is either (a) before the birth pulse or (b) after the birth pulse. The animals sampled at times t and $t+1$ are boxed, with N_i representing number of individuals in each stage class j. This example assumes that animals stay in each stage for only one time step, except that those in the last stage can survive and remain in that stage for multiple time steps. Fecundity for each age class (m_j) represents the average number of offspring born to each individual of N_j. The probability of survival through one time step is represented by P_j. To the right of each schematic is the resulting projection matrix and population-size vector. In (a), note that newborns (N_0) are not seen until they have survived through their first year (P_0) to be counted as N_1 at the next sample interval; likewise, individuals in age class 1 (N_1) are just about to become 2 years old, and so on. The next batch of N_0 individuals are born just after sampling. In (b), note that there is an extra column and row in the post-birth-pulse matrix (compared to the case of the pre-birth pulse) because post-birth sampling occurs just after reproduction, making N_0 recognizable as its own class.

we sampled on May 30 (just before the birth pulse), then the youngest age class counted would be the calves born last May 31 that had lived to be counted just as they are about to become 1 year old. The reproductive contribution for each stage class, then, must include not only stage-specific fecundity (m_j; the average number of female calves born per year per female in stage j) but also the probability of newborns surviving to be counted at the end of their first year (call this P_0). Now, what if instead of sampling on

May 30 we sample on June 1, the day after the birth pulse? In this case we would sample newborns. We would know exactly how many female calves were born per female, but some of the mothers alive last year would have died during the year (remember again that the goal is to project the population forward through time). Thus the reproductive-contribution elements of the top row would include stage-specific fecundity (m_j) as well as survival of mothers in that stage to have the newborns (P_j).

People who spend a lot of time messing with population-projection matrices often denote as F_j each element of the top row, where each element is this composite of fecundity and survival of either the mothers or the newborns. Thus each element of the top row of the matrix represents the reproductive contribution to the next time step under either

- pre-birth-pulse sampling, $F_j = m_j P_0$, or
- post-birth-pulse sampling, $F_j = m P_j$

So **post-birth** models have an extra stage class, because the newborns are recognizable as their own class (they were born just before sampling), whereas with **pre-birth**-pulse sampling we do not see newborns until they become class N_1 (as in Fig. 7.2a). I've been a little excruciating in detailing these two model types because it turns out to be a confusing topic in many ecology textbooks and published papers. If the accounting is kept straight, though, the two approaches give exactly the same population growth rate. And the strict pre- versus post-birth-pulse sampling can be relaxed to account for varying periods between the birth pulse and the sampling, or even to allow for continuous breeding (see Further reading). The development of the matrix for the common frog is shown in Fig. 7.3.

Projecting a matrix through time

How to project the matrix

Once the matrix model is filled with vital rates, it can be projected through time. The advantage of a matrix approach over the nonstructured models of the previous two chapters is that it keeps track of not just the total population size but also the numbers in each stage. In matrix terms, we will project through time the population-size vector. A vector is a skinny matrix of one column and k rows that contains the number of individuals in each of the k stages. To determine the population-size vector next year [$n(t+1)$], multiply the matrix M of vital rates by the vector of individuals at time t, $n(t)$:

$$n(t+1) = M * n(t) \tag{7.1}$$

By convention, matrices and vectors are shown in bold.

How do you multiply a matrix by a vector? Go across each row of the matrix, multiplying each element j by the same element of the vector (Fig. 7.4). Add up the products for one row to obtain the total number of individuals in that element of the vector. Again, if the math intimidates you, take a breath and realize that the projection
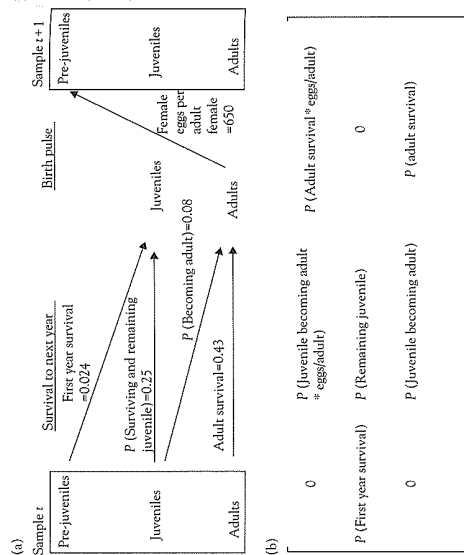
(a)

(b)

$$\begin{bmatrix} 0 & P(\text{Juvenile becoming adult} * \text{eggs/adult}) & P(\text{Adult survival} * \text{eggs/adult}) \\ P(\text{First year survival}) & P(\text{Remaining juvenile}) & 0 \\ 0 & P(\text{Juvenile becoming adult}) & P(\text{adult survival}) \end{bmatrix}$$

Fig. 7.3 A real-life example of a female-based post-birth-pulse matrix model for the common frog (Fig. 7.1). Female eggs per adult female refers to fecundity (see Box 4.8). (a) A diagramatic representation of the model; (b) the matrix (try plugging in the values and make sure you get the matrix in Fig. 7.1). Note that the matrix shows reproduction for juveniles (row 1, column 2) as well as adults (row 1, column 3) because a portion of the juveniles transition during the time step to become adults, at which point they reproduce. In general, for post-birth-pulse models for iteroparous species with n reproductive stages there should be $(n+1)$ non-zero elements in row 1.

of a matrix makes biological sense. The number of individuals in the first stage (newborns) next year comes from the reproductive contribution of each stage to the next time step (the top row of the matrix) multiplied by the number of individuals in each stage (the population vector). Likewise, the number of individuals advancing to a different stage or staying in the stage at the next time step are the product of survival (or other possible transitions below the first row) and the number of individuals in that stage.

Stable stage distribution and reproductive value

Matrix-projection methods can start with any number of individuals in different stages, and keep track of the relative number in each stage as well as population growth over time. This feature makes an important tool for many applications, ranging from tracking the possible growth of a translocated population to predicting what
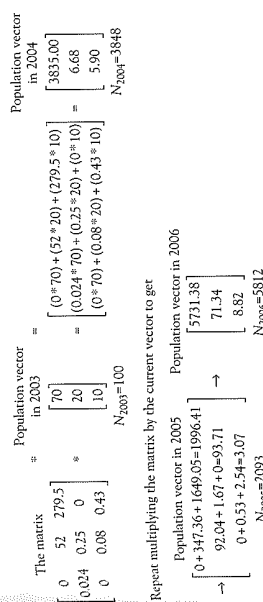
The matrix   Population vector in 2003

$$\begin{bmatrix} 0 & 52 & 279.5 \\ 0.024 & 0.25 & 0 \\ 0 & 0.08 & 0.43 \end{bmatrix} * \begin{bmatrix} 70 \\ 20 \\ 10 \end{bmatrix}$$

$$N_{2003}=100$$

$$= \begin{bmatrix} (0*70)+(52*20)+(279.5*10) \\ (0.024*70)+(0.25*20)+(0*10) \\ (0*70)+(0.08*20)+(0.43*10) \end{bmatrix}$$

Population vector in 2004

$$= \begin{bmatrix} 3835.00 \\ 6.68 \\ 5.90 \end{bmatrix}$$

$$N_{2004}=3848$$

Repeat multiplying the matrix by the current vector to get

Population vector in 2005

$$\begin{bmatrix} 0+347.36+1649.05=1996.41 \\ 92.04+1.67+0=93.71 \\ 0+0.53+2.54=3.07 \end{bmatrix}$$

$$N_{2005}=2093$$

Population vector in 2006

$$\rightarrow \begin{bmatrix} 5731.38 \\ 71.34 \\ 8.82 \end{bmatrix}$$

$$N_{2006}=5812$$

Fig. 7.4 An example of how to project a matrix through time. The sample matrix comes from the common frog (see Figs 7.1 and 7.3). A matrix of mean vital rates is projected for three time steps, beginning in the year 2003. Initially, our population has 70 pre-juveniles, 20 juveniles, and 10 adults. At the bottom of each vector is the total population size (N) for that year, rounded to the nearest whole female animal (as this is a female-based matrix).

might happen to certain stages during harvest. Although you can start with whatever number of individuals you want in each stage class, if vital rates stay relatively constant over time the population will converge on a population growth rate and stage distribution that is characteristic for that particular matrix. As a demonstration, Fig. 7.5 shows the projections for frogs from Fig. 7.4 for 14 years from the initial vector in 2003. By 2017 the population growth rate per year has become constant ($\lambda=1.46$; calculated by N_{t+1}/N_t). Also, the proportion of individuals in each class is constant, with about 98% of the population being pre-juveniles [e.g. (306,931/313,490) * 100=98%], 1.9% juveniles, and 0.2% adults (for practice, calculate the age distribution for the year 2016 from the information in Fig. 7.5). This constant proportion of individuals in each stage class is known as the **stable age distribution** (SAD) or, more generally, the **stable stage distribution** (SSD). Nearly any population matrix – whether it represents a declining, increasing, or stationary population – will converge on a constant population growth and SSD if the vital rates making up the matrix stay relatively constant[4]. (The time to SSD depends on factors such as the initial age structure and the characteristics of the matrix itself, but should be achieved within 20 time steps or so for most vertebrate populations.) The population growth rate at SSD, and the SSD itself, are characteristic of the matrix, and are independent of the initial age distribution.

Although the SSD and λ_{SSD} are independent of initial stage distribution, the distribution of animals across stages influences both the time to reach SSD and the population abundance in the future. Consider population growth curves for our frogs again,

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[4] There are matrices that will not converge to an SSD, including matrices that have only a single non-zero element in the first row, which can lead to stable oscillations (Leslie 1945, Caswell 2001).
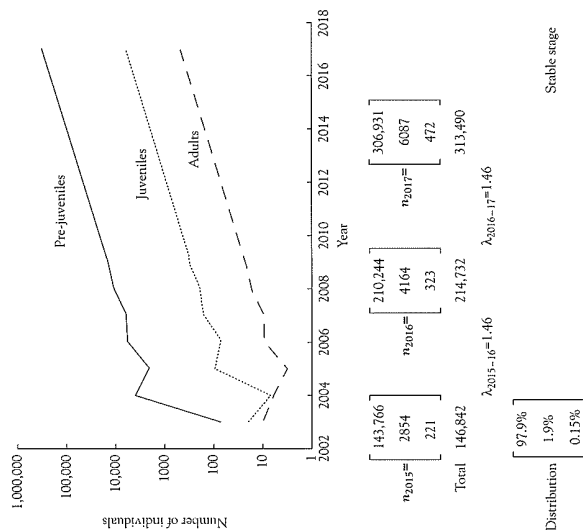
$$n_{2015} = \begin{bmatrix} 143{,}766 \\ 2854 \\ 221 \end{bmatrix} \quad n_{2016} = \begin{bmatrix} 210{,}244 \\ 4164 \\ 323 \end{bmatrix} \quad n_{2017} = \begin{bmatrix} 306{,}931 \\ 6087 \\ 472 \end{bmatrix}$$

Total 146,842   214,732   313,490

$\lambda_{2015-16} = 1.46$ $\lambda_{2016-17} = 1.46$

$$\text{Distribution} \begin{bmatrix} 97.9\% \\ 1.9\% \\ 0.15\% \end{bmatrix} \quad \text{Stable stage}$$

Fig. 7.5 Convergence to a SSD for the common frogs considered in previous figures. Population numbers over 14 years (from 2003 to 2017) are shown by stage class. The number of frogs is plotted on a logarithmic scale to accommodate the huge numbers of pre-juveniles, and because at SSD the trajectories become linear. Below the graph are the vectors (**n**), total population sizes, and geometric growth rates (λ) for the final 3 years. When the population reaches SSD, both the population growth rate (λ) and the proportion of individuals in each stage remain constant.

this time plotting total population size for 14 years with populations of 100 frogs that are seeded with all of one stage: 100 pre-juveniles, 100 juveniles, or 100 adults (Fig. 7.6). Even though all three populations start with the same initial number of frogs and the same constant set of vital rates, and after 14 years have all achieved the same growth rate at SSD, the numbers of frogs at time step 14 are vastly different for the three populations. Why? Because all stage classes are not created equal in their contribution to population growth, a phenomenon quantified by the concept of **reproductive value**. In Fig. 7.6 you can see that a population founded with 100 frogs, all adults, would reach a size of 2,125,660 frogs in 14 years, in contrast to the 477,171 individuals in the juvenile-seeded population and 7,843 in the population begun with 100 pre-juveniles. By convention, reproductive value is scaled relative to that of the first age
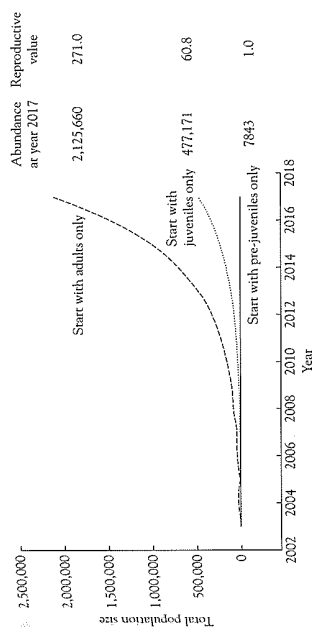
---

	Abundance at year 2017	Reproductive value
Start with adults only	2,125,660	271.0
Start with juveniles only	477,171	60.8
Start with pre-juveniles only	7843	1.0

Fig. 7.6 A demonstration of reproductive value by projecting common frog population size beginning with 100 adults, 100 juveniles, or 100 pre-juveniles, with the constant vital-rate matrix from Fig. 7.1. Although the initial abundance, the projection matrix, and eventual population growth rate and SSD are identical in each case, the initial stage distribution causes bounce in population growth early on, and leads to drastic differences in abundance. Reproductive value is typically scaled relative to the first age class. The right side of the graph shows how reproductive value can be calculated based on relative abundances at SSD, dividing each abundance by that of the population begun with the first age class. (I used abundances in year 2017, after 14 years had passed, but you could use abundances any time after SSD was achieved.)

class. Therefore, for the frogs, adults have a reproductive value of 271.0, and juveniles of 60.8, compared to the reproductive value of 1.0 for pre-juveniles (Fig. 7.6).

Because the reproductive value quantifies how much each stage acts as a seed for future population growth (Caswell 1989:67), it has immense yet under-appreciated applications in wildlife population biology. Reproductive value is not a synonym for fecundity, or reproduction in the top row of the matrix. Rather, it takes into account reproductive output at that stage, as well as future reproduction, the likelihood to survive to those stages, and the population growth rate. In other words, reproductive value is a weighted average of present and future reproduction, accounting for population growth rate, that provides us with a practical way to assess contribution of different stages to future population growth (see Lanciani 1998, Case 2000).

So, here's what we've got so far on projecting matrices: Because all stages are not equal in their effects on population growth – that is, they have different reproductive values – the initial age distribution affects future abundance and the time required to reach SSD[5]. It also causes the population size to bounce around early on (as the age

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[5] Look back at Fig. 1.3, showing how population momentum would cause the global human population size to increase even if women had only replacement numbers of children. The momentum is caused by an age structure leading to lots of babies even though modified vital rates would lead one to expect stationary population growth.

Box 7.1 How to calculate reproductive value, SSD, and the expected population growth at SSD

Because any constant population-projection matrix attains a constant SSD and λ, with each stage having a characteristic reproductive value, these are called **asymptotic matrix properties**. In the text I showed an approach to calculating each of the asymptotic matrix properties. For SSD and λ, project any initial population vector out by a number of times, say 100 time steps, and then calculate at time step 100 the proportion of individuals in each stage and the growth rate ($\lambda = N_{100}/N_{99}$). For reproductive value, you could use the seeding method (as in the frog example in Fig. 7.6).

Although these projection-based approaches are perfectly legitimate, intuitively transparent, and pretty easy to accomplish with simple multiplication that could be done, for example, in a Microsoft Excel spreadsheet, there are more elegant approaches to calculating the asymptotic matrix properties. For example, the **dominant eigenvalue** of the matrix, calculated using matrix math, equals λ, and its associated **right eigenvector** equals the SSD vector. Likewise, the **left eigenvector** of the dominant eigenvalue gives the vector of reproductive values.

distribution settles down to a SSD), and this is in the absence of any demographic or environmental stochasticity. However, the SSD and corresponding growth rate are a function of the matrix values and not the initial age distribution, so a population of any composition will eventually reach SSD and its associated λ as long as the matrix rates are relatively constant. Various ways to estimate reproductive value, SSD, and its associated λ value are described in Box 7.1.

For wildlife population management the implications of these population dynamics properties are profound. First, a set of vital rates represented as a projection matrix, coupled with a count of animals by stage class, provides insights into the inherent growth rate to be expected and the proportion of individuals eventually expected in each stage class over time. Second, the effect of age distribution means that a newly reintroduced population can be wildly erratic in its population growth – even without any stochasticity occurring – if the initial composition of the population is far from the expected SSD. Third, the reproductive value itself conveys the consequences of losing individuals of certain stages through harvest, or gaining them through translocations.

Before leaving this discussion on projecting matrix models through time, I should emphasize that I have only talked about density-independent matrix models. Density dependence can be added to matrix models (see the Further reading section of this chapter). I have also limited the discussion so far to the case where vital rates in the matrix are constant through time. Next I will briefly show how random variation (demographic and environmental stochasticity) can be incorporated into matrix projections.

Adding stochasticity to a matrix model

Although asymptotic properties such as the reproductive value, SSD, and population growth at SSD are useful, they are based on vital rates in the matrix being constant, or nearly so. But we know that vital rates are seldom constant for any length of time. And as we saw in Chapter 5, stochasticity has important implications, including the fact that it will decrease the likely future growth of a population compared with that expected from λ at the SSD[6].

Fortunately, computers make it quite easy to project a stage-structured model incorporating both environmental and demographic stochasticity (Chapter 5), assuming you have a specified starting population vector, and estimated means and variances for vital rates. To incorporate environmental stochasticity over time for a population, the computer builds a new matrix each time step, where each element in the matrix is chosen from a set of random numbers with a specified mean and process variance. The distribution of random numbers may be from a uniform distribution (all values equally likely to be chosen between a high and low value) or – more usually – from a distribution with central tendency, such as lognormal, normal, or beta (see Morris & Doak 2002). An alternate approach randomly picks one of several vital rates measured in the field (or even entire matrices of vital rates from field data; Bierzychudek 1982, Akçakaya 2000). Box 7.2 gives an example of environmental stochasticity in action for a population projection for the red-legged frog.

Demographic stochasticity in survival can be modeled to capture the real-world phenomenon whereby animals live or die as whole animals and not as fractions (Chapter 5). A common way to model demographic stochasticity in survival using the computer is to determine the fate of each individual in a stage based on the mean survival rate. Specifically, for each individual the computer picks a random number between 0 and 1; if the random number is less than the mean survival probability (also between 0 and 1) then the animal lives, if not, it dies. For example, suppose that your population vector has six yearlings, and the mean survival probability for yearlings is 0.8. Without demographic stochasticity, the expected number of subadults next time step is ($0.8*6=4.8$). With demographic stochasticity, the computer might pick the following six random numbers: 0.32, 0.89, 0.51, 0.11, 0.94, 0.70. Thus, four of the animals would live, but two would die (the second and fifth). At small numbers the proportion of survivors can deviate greatly from that expected from the mean survival rate, just as a small number of coin tosses can lead to a big deviation from 50:50 heads/tails (see Chapter 5).

Sensitivity analysis

As we have seen, all stage classes are not created equal in their management importance, their effects on population growth, or in their relative abundance. Similarly, it

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[6] Specifically, stochasticity will decrease population growth by an amount depending on which rate varies, how much it varies, and the sensitivity of λ to changes in that rate (Morris & Doak 2002:239). We will look at how to quantify sensitivity in the next section.

should not be surprising to learn that the vital rates themselves also vary widely in their effects on population growth and structure: all vital rates are not created equal. Intuition alone is insufficient to predict how changes in individual life-history components will affect population growth. Although one commonly hears conclusions like "forest fragmentation affects adult survival" or "acid rain affects clutch size," such statements do not indicate how the expected changes in vital rates affect population growth.

This simple demographic fact – that different vital rates do not have equal impacts on population growth rate – has been known for a long time (e.g. Cole 1954). But it was Hal Caswell's book on *Matrix Population Models* (1989), arriving on the heels of unprecedented access to desktop computers, that irrevocably convinced ecologists of the importance of a formal framework evaluating the effects of changes in vital rates. Sensitivity analysis provides that framework in the form of analytical and simulation-based tools to evaluate how past or future changes in life-history attributes or demographic vital rates affect population growth or persistence.

One of the earliest and most influential uses of sensitivity analysis in animal population biology targeted loggerhead sea turtles, which had been declining in the Atlantic by 3–5% per year for a long time. On the east coast of the USA enormous public sentiment built up concerning mortality of the eggs on the beach and the tiny (and adorable) hatchlings that were killed by predators, crushed by vehicles, and disoriented by lights as they tried to make their way from the nest to the ocean. Therefore, management focused on what seemed to be the obvious solution: increasing the survival of eggs and hatchlings. But in 1987 Deborah Crouse and colleagues published a sensitivity analysis that showed that even large increases in egg or hatchling survival would do little to reverse the population decline: the key was to increase survival of young adults in the ocean. It turned out that roughly 50% of loggerhead mortality in the Atlantic was due to young adult turtles becoming entangled in shrimp nets. The paper by Crouse et al. (1987) was key to the development of legislation requiring turtle-excluder devices to be installed by shrimpers (Crowder et al. 1994). In this case, sensitivity analysis of a matrix-projection model showed that intuition focusing on eggs and hatchlings alone to recover the species was wrong, and that a different management action would be much more beneficial and efficient for recovery.

Three main approaches are used by applied wildlife population ecologists to conduct sensitivity analyses (see Mills & Lindberg 2002 for more details). I will give a brief overview of these approaches, followed by a peek into the range of questions that can be answered with sensitivity analysis of matrix population models.

How to do a sensitivity analysis

Manual perturbation

The most basic approach to sensitivity analysis is to manually perturb, or change, the input to a population model and observe how the change affects the output.[1]

[1] Output could be population growth rate, or it could be probabilities of quasi-extinction (see Chapter 14).

Box 7.2 An example of how to model environmental stochasticity, based on a population-projection matrix for red-legged frogs (*Rana aurora*)

Notice that this is a different frog species than the one discussed previously in this chapter. Data come from Biek et al. (2002).

Step 1: here is the matrix of vital rates.

$$
\begin{bmatrix}
0 & \text{Probability of juvenile becoming adult * probability of laying * clutch size} & \text{Adult survival * probability of laying * clutch size} \\
\text{Embryo survival * larval survival * metamorph survival} & \text{Probability of remaining a juvenile} & 0 \\
0 & \text{Probability of juvenile becoming adult} & [\text{Adult survival}]
\end{bmatrix}
$$

Step 2: environmental stochasticity for the two emboldened vital rates (clutch size and adult survival) is as follows.

	Clutch size	Adult survival
Mean	303	0.69
SD	95	0.13
Distribution for random numbers	Lognormal	Beta

Step 3: for five time steps, the vital rates chosen randomly from the specified distributions might, for example, be as follows.

Time step	Clutch size	Adult survival
1	287.6	0.66
2	326.8	0.71
3	252.0	0.93
4	382.9	0.55
5	251.9	0.60

Step 4: the distribution of vital rates chosen many times would look like the graphs below.

For example, one could ask how the deterministic population growth rate (λ) of a matrix model changes when adult survival is increased by 10% compared with an increase in fecundity. Management options can be explored by comparing the expected effects on population growth or persistence when each option changes certain vital rates by any pre-determined amount. The approach is infinitely flexible; sensitivity analysis via manual perturbations is not limited to investigating the importance of vital rates alone, but rather can explore a range of factors including density dependence, inbreeding depression, and movement among populations (Chapter 12). Also, manual-perturbation sensitivity analysis can incorporate different age or stage structures, quantifying the effect of age structure on population growth.

Analytical sensitivity and elasticity analysis

You have learned that different age classes may have very different relative abundances at SSD, and different effects on future population size (i.e. different reproductive values). Therefore, a vital rate for a certain age class will influence λ more if there are proportionally more of that age class (larger SSD) and if each individual of that age class has a larger impact (bigger reproductive value). Analytical **sensitivities and elasticities** elegantly combine the reproductive value of an age class with its expected SSD to evaluate how infinitesimal changes in individual vital rates will affect λ. Specifically, sensitivity for a vital rate that makes up matrix element a_{ij} (remember this is the matrix element in row i and column j) is a function of the reproductive value of the age class (v_i) and the SSD (w_j)[8]:

$$\text{Sensitivity of matrix element } a_{i,j} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\left(\displaystyle\sum_{k=1}^{\text{Last stage class}} v_k w_k \right)} \tag{7.2}$$

A larger reproductive value (v_i) or SSD (w_j) leads to a larger sensitivity. Notice that sensitivity is a partial derivative, defined as the infinitesimal absolute change in population growth rate given an infinitesimal absolute change in a vital rate or matrix element, while all other vital rates are held constant. As an alternative to the calculus in eqn. 7.2, you can also estimate sensitivity by making a tiny manual change to the vital rate of interest, and quantify how λ changes before and after the perturbation. For example, increase the element a_{ij} by 0.01, leaving everything else unchanged, and estimate λ before and after, as follows.

---

[8] If you prefer to think about equations graphically, consider that as a partial derivative, the sensitivity of matrix element a_{ij} equals the slope of the tangent to the curve relating population growth rate to the matrix element, evaluated at the mean element.

$$\text{Sensitivity of matrix element } a_{i,j} = \frac{\lambda_{a_{ij}+0.02} - \lambda_{\text{original}}}{0.01} \tag{7.3}$$

So, for the red-legged frogs in Box 7.2, analytical sensitivity would quantify how a tiny change in juvenile survival (say, from 0.69 to 0.70) would affect population growth compared with the same tiny change in another vital rate, such as clutch size (from 303 to 303.01). Although this may be useful for some applications, you can see immediately that from a practical perspective we have a scaling problem; the same absolute change of 0.01 in the mean of these two rates is very different for survival (a 1.4% change) compared with clutch size (a 0.003% change). That's where elasticity becomes useful. Elasticity is sensitivity's cousin, a metric that rescales the sensitivity to account for the magnitude of the vital rate. Thus elasticities are **proportional sensitivities** that describe the proportional change in λ given an infinitesimal one-at-a-time proportional change in a vital rate[9]:

$$\text{Elasticity of matrix element } a_{i,j} = (\text{sensitivity of } a_{i,j}) * \frac{a_{i,j}}{\lambda} \tag{7.4}$$

When matrix elements are composed of more than one vital rate (e.g. where each element of the top row of a projection matrix contains both reproduction and survival components), or when a particular vital rate shows up in more than one matrix element, component sensitivities and elasticities can be calculated for each vital rate that appears in one or more matrix elements. Although the analytical formula for component sensitivities requires chain-rule differentiation for each a_{ij} that contains a particular vital rate x, in many cases the procedure is pretty simple[10].

As a proportional measure of sensitivity, analytical elasticities are more widely used in applied population biology than sensitivities. Elasticities can be added together to predict the joint effect of changes in multiple rates (assuming the changes in vital rates and λ are linearly related). Elasticities of all matrix elements sum to one; elasticities of component vital rates do not add up to one but can still be ranked. Based on analysis of measured vital rates from hundreds of studies of different bird and mammal species, predictable patterns link life-history traits to the relative elasticities of different vital rates (Box 7.3).

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[9] Analogous to sensitivity, elasticity is the slope of the tangent to the curve relating proportional changes in λ to proportional change in matrix elements.

[10] Assuming that each matrix element is a simple linear combination of different vital rates, here is a simple translation of the chain rule to calculate sensitivity for a vital rate x that is a component of more than one matrix element, where each element containing x has sensitivity s_{ij},

$$\sum_{\substack{\text{Elements containing } x}} [(s_{i,j}) * (\text{product of components other t}$$

You can also use eqn. 7.3 to tweak a component vital rate and calculate sensitivity. Either way, the

elasticity of vital rate $x = (\text{component sensitivity of vital rate } x) * \left(\dfrac{x}{\lambda}\right)$.

Box 7.3 How might we predict which vital rates will have highest elasticities for a wildlife species?

Although the best way to assess elasticity of a vital rate is to conduct analysis on a complete set of field-derived vital rates for a particular population, it is useful to know that some coarse generalizations can support general principles. For example, species with early maturation and large litters tend to have elasticities that are higher for reproduction (litter size and offspring survival) and lower for adult survival: conversely, in species with late maturation, fewer offspring, and higher survival rates, population growth is affected more by adult survival than by reproduction (Heppell et al. 2000, Saether & Bakke 2000, Oli & Dobson 2003). Survival of all stages will tend to have higher elasticities than reproductive output for most taxa with lifespans longer than a year (Crone 2001). The implication is that "in any sharp change of population growth rate for a long-lived species, one should first suspect a change in adult survival" (Lebreton & Clobert 1991:108).

Although these life-history general principles give us first-cut insights into which rates will have the highest elasticities, that does not mean that those rates are most important. Remember, vital rates with low elasticities but that change a large amount could actually affect the growth rate more than rates with high elasticities but that change little.

Analytical sensitivities and elasticities are easily applied, comparable across studies, and can be calculated from a single population matrix constructed from average or even best-guess vital rates. However, we should keep in mind their fundamental assumptions (Mills et al. 1999, 2001). First, they are asymptotic, relying on the population being at SSD (although this assumption can be relaxed; see Fox & Gurevitch 2000, Grant & Benton 2000, Caswell 2001). Second – and perhaps most importantly – analytical sensitivities and elasticities by themselves say nothing about how much vital rates change in nature or under management.

A classic case in point (Gaillard et al. 1998, Raithel et al. 2006) is that for ungulates in general, adult survival would be expected to have the highest elasticity by far. However, juvenile survival will be much more variable than adult survival, because juveniles are less buffered against density-dependent influences or environmental factors such as predation, bad weather, and so on. The fact that juvenile survival may easily vary from 0.1 to 0.7, whereas adult survival will tend to be much less variable, means that the rate with relatively low elasticity that changes a lot (e.g. juvenile survival) may affect population growth more than a rate with high elasticity that doesn't vary much (e.g. adult survival). Elasticities based on a mean matrix cannot capture how much a vital rate, and therefore population growth, can change in nature or under management.

An extension of analytical sensitivity and elasticity analysis, called **life-table-response experiments** (or LTREs for short), does explicitly account for variation with an analytical equation (Caswell 2001). For practical purposes, changes simulated on the computer are a more versatile way to the same end, so I will discuss such an approach next.

Life-stage simulation analysis

Wisdom and Mills (1997) developed a simulation-based approach to sensitivity analysis that might be considered a hybrid of the manual perturbation and analytical sensitivity/elasticity-based methods. The approach is called **life-stage simulation analysis** (LSA; Wisdom et al. 2000)[11] because it uses simulations to evaluate the impact of changes in different vital rates on elasticity rankings and λ. For the purposes of conservation decision-making, the user obtains (from the field if possible) both means and variances for vital rates. The variance should be based on process variance, uninflated by sample variance (Mills & Lindberg 2002). For projecting what might happen in the future, you can couple information from the past with specified changes in means and variances that are considered biologically, politically, and logistically possible under management in the future[12]. Correlations among vital rates are specified, if possible, as are the distribution functions for each vital rate (i.e. uniform, lognormal, beta, etc.). A computer program constructs many matrices with each rate in each matrix drawn from the specified distributions. Population growth rate is calculated for the matrix (usually asymptotic λ at SSD, although stochastic λ could also be calculated).

Output metrics in LSA include elasticity-based measures (e.g. the proportion of replicates where the vital rates shift rankings of elasticities, or the differences in elasticity values whenever the rankings of elasticities change across the replicates; Wisdom et al. 2000), as well as other metrics that avoid elasticity entirely. For example, one LSA output could be the percentage of replicates having positive population growth under different scenarios (Fig. 7.7).

Another way that LSA has commonly been used to evaluate the importance of vital rates for management is to regress λ on each vital rate as all rates change simultaneously (including the vital rate of interest) in 1000 or so simulated matrices (e.g. Wisdom & Mills 1997, Crooks et al. 1998, Cross & Beissinger 2001). The coefficient of determination (R^2) represents proportion of the variation in population growth rate that is explained by environmental variation in that vital rate, with all other vital rates varying simultaneously. When all main effects and interactions are included, the R^2 values sum to one. When λ is a linear function of the vital rates, the slope of the line equals the analytical sensitivity and R^2 is a function of both the slope (i.e. analytical sensitivity) and the proportionate variation in that vital rate, adjusted for covariance among vital rates. The same relationships hold for elasticity if the regression is done on log-transformed data (Brault & Caswell 1993, Horvitz et al. 1997). Therefore, the

[11] Morris & Doak (2002:344–8) refer to this approach as a "simulation-based sensitivity analysis."

[12] I avoid use of the terms prospective and retrospective sensitivity analysis (Caswell 2001) because these terms have been used to imply that the inclusion of variation in a sensitivity analysis prohibits one from asking what might occur under future management. When conducting a sensitivity analysis of potential management scenarios, it seems more constructive to simply make explicit whether or not variation is included, the origin of the estimates of both variation and mean rates, and the rationale for potential future changes in vital rates (Mills et al. 2001, Wisdom et al. 2000, Mills & Lindberg 2002).
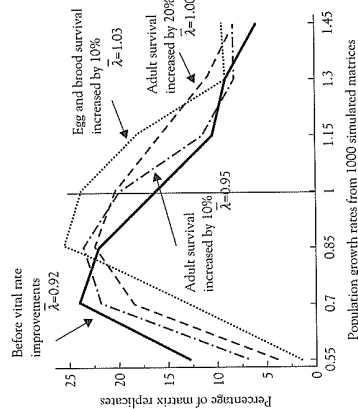
Fig. 7.7 An example of one form of LSA output for greater prairie-chickens, a species whose populations are declining, scattered, and potentially vulnerable to extirpation (see Wisdom & Mills 1997). The potential consequences to expected population growth (λ) for different potential management strategies are derived from simulations of mean (and variances) of vital rates using a LSA. The expected distribution of λ in 1000 simulated matrix projections before vital rate improvements is shown by the solid line; dashed and dotted lines show how the distribution of expected growth rates change as particular vital rates are improved by increasing their means by specified amounts (and decreasing their variation by 20%). $\overline{\lambda}$ gives the mean of the λ for that distribution. Increasing by 10% the average survival during part of the first year (egg and brood survival) gives the biggest increase in the expected population growth (dotted line). Increasing by 10% the average adult survival gives much less improvement (dotted/dashed line). To get about the same increase in population growth as the 10% increase in first-year survival, average adult survival would need to be increased by 20% (dashed line). Modified from Wisdom et al. (2000). Reproduced with permission of the ESA.

simulation-based LSA R^2 can be compared with analytical life-table-response experiment approaches, in that both account for infinitesimal effects (e.g. elasticity) as well as the range in variation of different rates (Wisdom et al. 2000). However, LSA is more flexible than life-table-response experiments because any sort of change can be simulated, and a variety of output metrics are possible.

Case studies

To end the chapter, I will consider four case studies that used the application of matrix projections and sensitivity analysis to inform management, often in nonintuitive ways.

Case study 1: what are the best management actions to recover an endangered species?

Red-cockaded woodpeckers are an endangered species endemic to mature pine forests of the southeastern USA. They are cooperative breeders, with males staying on natal territories as nonbreeding helpers to the breeding pair for up to 11 years before inheriting natal territories or dispersing. How should managers decide which management strategies are most likely to increase the population growth of this endangered species? Detailed field studies provided critical insights into vital rates, behavior, and potential effects of management actions (Walters 1991), which could then be extended with population models exploring how population growth and persistence could be most efficiently increased through management.

Selina Heppell and colleagues (1994) used an innovative matrix-modeling approach based on male red-cockaded woodpeckers and using behavioral transitions associated with helping in addition to the usual size or age transitions (Fig. 7.8a). For example, fecundity in the top row was defined as the number of fledglings produced by individuals that survived the year and were helpers or breeders in that time step. Four management strategies with specific predicted effects on one or more vital rates were evaluated using the manual-perturbation approach coupled with elasticity analysis. Each of these actions targeted specific vital rates, thereby affecting one or more elements a_{ij} of the matrix in Fig. 7.8(a). The management options were as follows.

1 Remove invaders: remove cavity invaders such as flying squirrels and other woodpecker species that inhabit red-cockaded woodpecker nest cavities, increasing woodpecker fecundity (all elements of top row).

2 Female translocation: capture and relocate female red-cockaded woodpecker fledglings to solitary male territories, causing more solitary males to become breeders (increase $a_{5,4}$ and $a_{1,4}$).

3 Cavities in occupied territories: drill cavities in existing territories, increasing the fecundity of breeders (increasing all of the top row) and the probability that fledglings become helpers ($a_{2,1}$) while decreasing the chance that fledglings become breeders ($a_{5,1}$).

4 Cavities in unoccupied territories: increase new territories by drilling artificial cavities in unused yet suitable habitat and by reducing hardwood understory. This action should increase both fledgling-to-breeder and helper-to-breeder transitions (top row, and $a_{5,1}$ and $a_{6,2}$) while decreasing fledgling mortality (all of first column).

What would be the predicted relative effect of these management actions? Creating new territories through cavity construction in unoccupied territories (management option 4) had the biggest benefit (Fig. 7.8b) through its effects on two vital rates with relatively high elasticity (fledgling-to-breeder and helper-to-breeder transitions). Removing cavity invaders and placing more cavities in unoccupied territories were also potentially reasonable approaches, whereas female translocation (option 2) seems a waste of money. Importantly, Fig. 7.8 also underscores a recurring theme: the best strategy ultimately depends on how much rates could be changed. For example, a 25% change by removing invaders (option 1) would increase red-cockaded woodpeckers more than a smaller (10%) change via the best strategy of installing cavities in unoccupied territories.

Fig. 7.9 An LSA-based approach to evaluating the relative importance of different vital rates to population growth in brown-headed cowbirds. The R^2 value describes the proportion of variation in λ explained by variation in a vital rate, based on 1000 simulated matrices where vital rates were chosen from the range of variation determined from published studies. Notice that egg survival alone accounts for 61% of the variation in λ. From Citta & Mills (1999)

hunters) are dispersed each year to protect and enhance wetlands and grasslands for waterfowl habitat. Traditionally, less than 40% of these funds has been apportioned to breeding areas. An ongoing debate has centered on how much effort (and money) should be dedicated to protection and enhancement of habitats on breeding areas (especially wetlands and nesting habitat) compared with non-breeding areas (especially wetlands for migratory and wintering waterfowl).

Hoekman et al. (2002) used LSA to assess the effects of management and environmental variation on population growth of the North American mid-continent mallard population, considering both the infinitesimal effect of each vital rate, and the observed variation in each. The LSA indicated that vital rates on breeding grounds (hen survival during the breeding season, clutch size and nest success, and survival of ducklings) collectively explained about 84% of the variation in λ, compared to only 9% explained by nonbreeding survival on migration and wintering areas[13] (Fig. 7.10).

The finding that the contribution to duck population growth of nonbreeding survival is dwarfed by vital rates on breeding grounds has profoundly influenced waterfowl management. An expert panel assembled in 2004 by the US Fish and Wildlife Service came to a striking science-based conclusion based largely on the sensitivity analysis: given that variation in vital rates on breeding grounds explains the vast majority of the variation in λ for mid-continent mallards, and given the general absence of strong differences in the ability to change vital rates on breeding compared with nonbreeding areas through habitat management, the panel recommended that approximately 90% of the waterfowl conservation funds should go to breeding areas (Cox et al. 2004). This suggestion has been elevated to the top levels of the US Fish and Wildlife Service, and although politics will certainly play a role, it appears likely that proportionately more management funding will shift to the breeding grounds. Simultaneously, current adaptive harvest management for waterfowl (see Chapter 14) is recognizing the need to incorporate breeding-area processes to optimize harvest management. Thus, a matrix population model has distilled a nonintuitive insight (that breeding-ground dynamics drive population growth) that is changing the trajectory of waterfowl funding and management. These results have also been useful in reassessing research priorities, with increased funding directed toward sources of variation in nest and duckling survival.

Case study 4: what research is needed to understand global amphibian declines?

Beginning around 1990, researchers from around the world sounded an alarm that amphibian numbers seemed to be declining. The call to action came from monitoring studies, and for the last decade or so the question has been how the declines would best be reversed. Work on a variety of species has shown how various vital rates might be affected by ultraviolet radiation, pH, disease, habitat destruction, or other factors. But there has been a missing link between the data showing declines and the data

Case study 3: how should a harvested species be managed?

Migratory waterfowl have been intensively studied and managed, to both protect populations and provide compatible hunting opportunities. In the USA about $50 million in migratory bird conservation funds (primarily funded by duck stamps bought by

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[13] The final 7% can be thought of as statistical noise, accounted for by interactions among rates and the nonlinear response of λ to the changes in vital rates.

Mid-continent mallard population: percentage contribution to variation in λ

Breeding incidence (R²=0.004)

Egg hatch rate (R²=0.004)

Clutch size (R²=0.02)

Nonbreeding survival (R²=0.09)

Renesting intensity (R²=0.05)

Duckling survival (R²=0.14)

Total R² (excluding nonbreeding survival) =0.84

Nest success (R²=0.43)

Breeding season survival (R²=0.19)

Fig. 7.10 Results of an LSA analysis for female mid-continent mallards in North America (Hoekman et al. 2002). Each pie slice shows the proportion of variance in population growth rate explained by that vital rate in 1000 simulations of vital rates drawn from field studies. In other words, the plot shows the R² from regression plots of vital rates against population growth determined as in the cowbird example (Fig. 7.9). Approximately 84% of the variation in population growth rate is expected to arise from breeding-ground vital rates. The 7% not accounted for in the pie can be thought of as statistical noise, accounted for by interactions among the rates and the nonlinear responses of population growth to the changes in vital rates.

showing that vital rates have changed by certain amounts: would those changes in vital rates be likely to cause the observed declines?

Biek et al. (2002) conducted sensitivity analysis for three potentially declining amphibian species for which there were reasonable vital-rate estimates and purported mechanisms driving reduced vital rates: western toads, red-legged frogs, and common frogs (the latter two species formed the basis for the matrix examples in this chapter). In all three species, post-metamorph survival (juvenile or adult) had the highest elasticity, indicating that λ was most likely to be decreased by a given reduction in these rates compared with others (such as embryonic or larval survival) that have been the target of most experimental studies. Manual perturbation and LSA enriched the

conclusions by reinforcing (as in other case studies) that if rates with low elasticities vary a lot, then they can affect λ even more than rates with higher elasticities.

Summary

Understanding the effects of age or stage structure on population processes is critical for wildlife population ecologists, both because different stages are important to management decision-making (e.g. bull elk compared with fawns, or turtle eggs compared with ocean-going juveniles) and because structure affects population growth. Matrix population models are certainly not the only way to account for population structure, but they are popular due to their relative simplicity and straightforward links to vital rates measured in the field.

The fact that different stages are not equal in their influence on population growth means that a savvy population ecologist will quantify the reproductive values of each stage to help inform translocations, harvest strategies, or control of pest species. If vital rates remain relatively constant over time, a population will achieve a SSD and a population growth rate characteristic of those vital rates.

Because both reproductive values and proportions in the population will differ between stages, survival and reproduction in different stages do not have the same effects on population growth. In other words, just as different stages are not equal in their effects on population growth, neither are vital rates equal. The broad and important field of sensitivity analysis seeks to quantify the relative importance of different vital rates and the expected efficacy of different management actions on population growth or persistence. Analytical sensitivity and elasticity show how much an infinitesimal change in each vital rate might affect population growth. As useful as this insight is, remember that the amount that a rate can change in nature or under management will also affect how important a vital rate is to population growth.

The two sensitivity analysis methods that do the best job of specifically and intuitively incorporating a specified range of variation in vital rates include manual perturbations and LSA. Manual perturbations of vital rates can contrast specific predictions from management actions that are expected to have specific effect, an approach that identified useful steps for managers to take in the recovery of red-cockaded woodpeckers. LSA can simulate many possible matrices from user-specified means and variances. Its output can be variable, including assessment of the stability of elasticity rankings across variation in vital rates as well as direct insight into how changes in certain rates are expected to affect population growth. Management of pest species (e.g. cowbirds), harvested species (e.g. mallards), and other species of concern (e.g. declining amphibians) would be more efficiently directed using LSA to evaluate the effects of management scenarios on expected population growth rate.

I will end with an apt metaphor borrowed from Ron Reynolds of the US Fish and Wildlife Service. A good general always goes into battle with a thoughtful focus on achieving the most with the resources at hand; troops are not scattered randomly across the battlefield or positioned according to political whims. Likewise, a good

wildlife manager should use the insights from population-projection models and sensitivity analysis to see how proposed actions could ripple through to affect population growth in ways that are not obvious, revealing which actions will be a waste of time and money and which would be cost-effective. Population-projection models frame the biological context to help win the management battle.

Further reading

Caswell, H. (1989/2001) *Matrix Population Models: Construction, Analysis, and Interpretation*, 1st and 2nd edns. Sinauer Associates, Sunderland, MA. The single most important reference for the mathematics of matrix models.

Noon, B.R. and Sauer, J.R. (1992) Population models for passerine birds: structure, parameterization, and analysis. In: *Wildlife 2001: Populations* (eds. D.C. McCullough and R.H. Barrett), pp. 441–64. Elsevier Applied Science, London. Although specifically focused on birds, this is one of the most readable and practical discussions of building and analyzing matrix populations.

Appendix D

Tools for assessing population trend and viability in greater sage-grouse

March 26, 2009

Yakima Valley Community College, Yakima, WA

J. Michael Scott[1], Jon S. Horne[2], Edward O. Garton[2], Brian Dennis[2], and Katherine Strickler[2]

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Tools for assessing population trend and viability in greater sage-grouse

Date: March   26, 2009

Location: Yakima Valley Community College, Yakima, WA

Host organizations: U.S. Geological Survey and University of Idaho, with funding from the Department of Defense's Strategic Environmental Research and Development Program (SERDP)

Host team: J. Michael Scott (USGS, Idaho Cooperative Fish and Wildlife Research Unit)
Oz Garton (University of Idaho)
Jon Horne (University of Idaho)
Katherine Strickler (University of Idaho)
Brian Dennis (University of Idaho)

Invited participants: Interested biologists and managers from Department of Defense, U.S. Fish and Wildlife Service, state game management agencies

Contact: Katherine Strickler, University of Idaho
(kstrickler@uidaho.edu, 208-885-4343)

Format: One-day workshop with presentations and hands-on software demonstration

Background: Estimation of a population's growth rate or trend is an important component of research and management for species of concern, as population increases or declines are often used to trigger management intervention. Population trend is a common method for evaluating species status because it uses estimates of abundance over time, which are often the only population data available. However, trend estimation is frequently challenged by factors such as missing counts, unknown variance in the data, or the need to select from a variety of statistical methods available for estimating trend using time-series abundance data. In this workshop, we will address issues and approaches for estimating population trend and viability in the greater sage-grouse (*Centrocercus urophasianus*). As sage-grouse populations have declined drastically across the western USA, they have become of increasing

management concern to federal and state agencies. Current levels of intense attention on sage-grouse management amplify the importance of accurately assessing population trend. Extensive abundance estimates, in the form of lek counts conducted for more than 50 years in some areas, are well suited for population trend estimation.

The objectives of the workshop are to: 1) review methods of estimating population trend and sensitivity, 2) introduce software programs developed at University of Idaho to estimate population viability (PopGrowth and MetaPVA), 3) present results of sage-grouse population trend and viability analyses, and 4) request feedback from participants regarding software products and analyses.

We will use sage-grouse management concerns at Yakima Training Center and surrounding areas to illustrate the utility of PopGrowth and MetaPVA to address questions relevant to management of sage-grouse throughout its range. In addition, we will present details of an ongoing, range-wide extinction risk assessment for greater sage-grouse. The workshop will include hands-on lab sessions to demonstrate the software programs as well as opportunities to discuss different ways the programs can be used to address specific management questions raised by workshop participants.

In this workshop we will describe and evaluate several stochastic growth models that can be fit to count data. When coupled with environmental covariates, these models can be used to predict population viability under different management scenarios. Further, estimation of population parameters derived from growth models can be used in sensitivity analyses to identify population characteristics that have the greatest influence on population viability.

We will introduce two new software programs that fit different population growth models and implement several methods of sensitivity analysis. In concert, PopGrowth and MetaPVA allow for selection of the most appropriate growth model for a particular data set, projection of population viability, and evaluation of the effect of different management actions on population persistence. PopGrowth models population trend by estimating relevant parameters of stochastic population growth models. After estimating model parameters, these estimates are then used in MetaPVA to infer population viability and identify the parameters to which population persistence is most sensitive.

Agenda: 0800-0900   Introduction and overview of population trend methods, software and analyses

0900-1000   Time series analyses: software and preliminary results

1000-1030 Discussion

1030-1130   Sensitivity analyses for metapopulation viability models: software and preliminary results

1130-1200 Discussion

1200-1330 Lunch   (provided)

1330-1530 Software   labs

1530-1630   Critique and discussion

1630-1700 W   rap-up

Population Viability Models

Concept: History

<u>Minimum Viable Population</u>

1. Leopold (1933:47):importance of recognizing "the minimum number of individuals which may successfully exist as a detached population."

2. MVP popularized by injunction from US Congress (NFMA of 1976) to US Forest Service: maintain "viable populations" of all native vertebrate species in each National Forest.

3. From being a legal / philosophical concept to scientific inquiry:

   By late 60's / early 70's: two relevant (but independent) avenues:

   a. demographic (MacArthur and Wilson 1967, Richter-Dyn and Goel 1972) : Critical "floors" for population size, below which population would quickly go extinct. Classic: Shaffer's work on grizzly bear MVP based purely on demo. & environmental stochasticity. (1983, 1985).

   b. Genetic issues

   Frankel (1974): Emphasized need and conditions for maintaining evolutionary potential of species: "The prime parameters are the level and distribution of variation, the size of the minimum viable population, and the optimal and minimal sizes of reserves. We need to know the minimum population size which is likely to yield a required level of variation."

4. Soulé and Wilcox (1980): first specific recommendations for MVP led to famous 50:500 rule.

   a. 50: minimum Ne to protect against short-term loss of fitness due to inbreeding, based on empirical observations

   Caveats that were often lost:

   - Ne, not N (Ne typically 1/5 to 1/3 N).

   - *short term* guideline for captive breeding and similar "holding operations", not to the long term survival of wild populations which would have many other factors affecting their persistence.

- based purely on genetic factors, not incorporating the other factors that would again increase the minimum necessary size for persistence.

  b. 500: estimated minimum genetic Ne where loss of additive genetic variation of a quantitative character due to genetic drift would be balanced by new variation due to mutations. → Range up to 5,000 or more.

MVP is problematic for both philosophical and scientific reasons.

   a) point estimate vs. embracing uncertainty

   b) ecologically effective vs. minimally viable

Population Viability Analysis

1. Gilpin and Soule (1986): "This chapter introduces the term 'population vulnerability analysis' (PVA) for analyses that estimate minimum viable populations (MVPs). That is, MVP is the product, and PVA the process."

2. By the 1987 Viable Populations for Conservation book: PVA had morphed into "Population Viability Analysis".

3. What is PVA?

   - 'Mills' definition: *the application of data and models to estimate probabilities that a population will persist for specified times into the future (AND to give insights into factors that constitute the biggest threats).*

Defining and describing "extinction":

Quasi-extinction threshold advantages

- Provides a lot more options than modeling for extinction!

- Allows you to finesse around the ignorance of how dynamics will change for your species at very low numbers (e.g., genetic stochasticity, demographic stochasticity, Allee affects, etc.).

"Extinction Vortex" (from Mills 2007)

Fig. 12.1 A simplified representation of the extinction vortex. The effects of deterministic stressors are filtered by the population's environment (habitat as well as variable extrinsic factors such as weather, competition, predators, and food abundance) and by its structure (including age structure, sex ratio, behavioral interactions, distribution, physiological status, and intrinsic birth and death rates). Each turn of the feedback cycle increases extinction probability (Gilpin & Soulé 1986). The extinction vortex model predicts that some small populations are more likely to become smaller and eventually go extinct with each generation due to the interaction of genetic and nongenetic factors. Modified from Soulé and Mills (1998). Copyright (1998) AAAS.

1. Count-based (i.e., time series of abundance)

2. Demographically explicit (based on vital rates)

Count-based population growth models

Population Growth in Unlimited Environments

- Overview (see Mills 2007:91 - 99)

Deterministic Exponential Growth Model

- Unlimited, constant, favorable environment (i.e., population growth rate remains constant).

- Age-specific birth and death rates remain constant (i.e., population has a stable-age distribution).

Discrete growth:

$$N_{t+1} = N_t \lambda$$

If the population continues to grow at the rate λ for "t" time steps from an initial abundance at time 0 (N_0), then at time t we would expect N to be:

$$N_t = N_0 * \lambda_1 * \lambda_2 * \dots \lambda_t$$

$$N_t = N_0 \lambda^t$$

Stochastic Exponential Growth Models (see Humbert et al. *in review*):

- **Stochastic:** involving a random variable; a random outcome

- A **random variable** (e.g., number of offspring) is one that can take more than one value in which the values are determined by probabilities.

- **Statistical Distributions** and random outcome (Examples: uniform, normal, log-normal)

Model 1: Exponential Growth Observation Error (EGOE)

- The oldest, and most predominantly used model results in a log-linear regression of counts against time, where the slope of the regression gives the population trend (e.g. Caughley 1977, Eberhardt and Simmons 1992, Gerrodette 1987)

- Actual population growth is *deterministic*

- Stochasticity arises only from imprecision of abundance estimates

$$Y_t = \ln(N_0) + \mu t + E$$

where Y_t = natural logarithm of observed (estimated) abundance; μ = instantaneous growth rate; $E \sim N(0, \tau^2)$

**Note: estimates of μ and τ can be obtained by linear regression of $\ln[n_t]$ against time (t).

$\hat{n}_0 = Exp[\text{y-intercept}]$

$\hat{\mu} = \text{slope}$

$\hat{\tau}^2 = \text{mean residual sum-of-squares}$

y = 0.1528x + 4.48
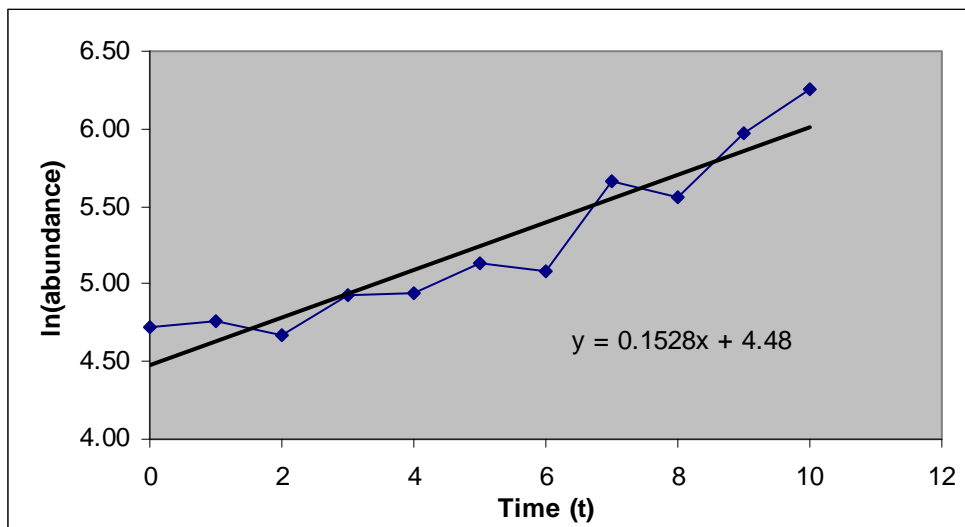
Model 2: Exponential Growth Process Noise (EGPN)

- Model often used to analyze population viability based on the exponential growth model (see Dennis et al. 1991, Cha. 3 Morris and Doak 2002)

- Actual population growth is stochastic

- 'Process' noise: environmental stochasticity bumps the population growth rate around at each time step

$$\ln\left(N_{t+1}\right) = \ln\left(N_t\right) + \mu + F$$

where $F \sim N\left(0, \sigma^2\right)$

- Parameters can be estimated (see Dennis et al. 1991) by linear regression, without intercept, of $y_i = \left[\ln(n_i / n_{i-1})\right] / \sqrt{s_i}$ as the 'dependent variable' and $\sqrt{s_i}$ as the 'independent variable'. Where, $s_i = t_i - t_{i-1}$

Model 3: Exponential Growth State Space (EGSS)

- Actual population growth is stochastic

- 'Process' noise and observation error induce stochasticity

$$\ln\left(N_{t+1}\right) = \ln\left(N_t\right) + \mu + F \qquad \text{actual abundance}$$

$$Y_{t+1} = \ln\left(N_{t+1}\right) + E \qquad \text{natural logarithm of observed abundance}$$

- Parameters can be estimated (see Staples et al. 2004) using maximum likelihood or restricted maximum likelihood (REML) . It has been our experience that REML estimates perform better.

Population Growth in Limited Environments

- Limited environments cause age-specific birth and/or survival rates to **decline** with increasing population size.

- Intraspecific competition causes growth rates to decline with increasing population size

Stochastic Logistic (Ricker) Growth Model

- Growth rate is a **decreasing** <u>**linear**</u> function of population size

$$\ln\left(N_{t+1} / N_t\right) = a + bN_t + F$$

where a = maximum growth rate at $N = 0$ (i.e., *Rmax*); b = effect of intraspecific competition

**Note if $b = 0$, this is the EGPN model

Stochastic Gompertz Growth Model

- Growth rate (i.e., birth rate and mortality rate) is a **decreasing <u>linear</u>** function of the **natural logarithm** of population size

$$\ln\left(N_{t+1} / N_t\right) = a + b \times \ln\left(N_t\right) + F$$

**Note: a can no longer be interpreted as *Rmax*… As N approaches 0, the growth rate approaches infinity (∞). a is the growth rate when abundance $= 1$.

Stochastic Theta-logistic Growth Model

- Growth rate (i.e., birth rate and mortality rate) is a **decreasing <u>linear</u>** function of population size **raised to the power theta (θ)**

$$\ln\left(N_{t+1} / N_t\right) = a + bN^{\theta}_t + F$$

Three situations arise:

1. $\theta = 1$: Ricker (logistic)-type density dependence

2. $0 < \theta < 1$: Growth rate versus N is a concave relationship (e.g., Gompertz)
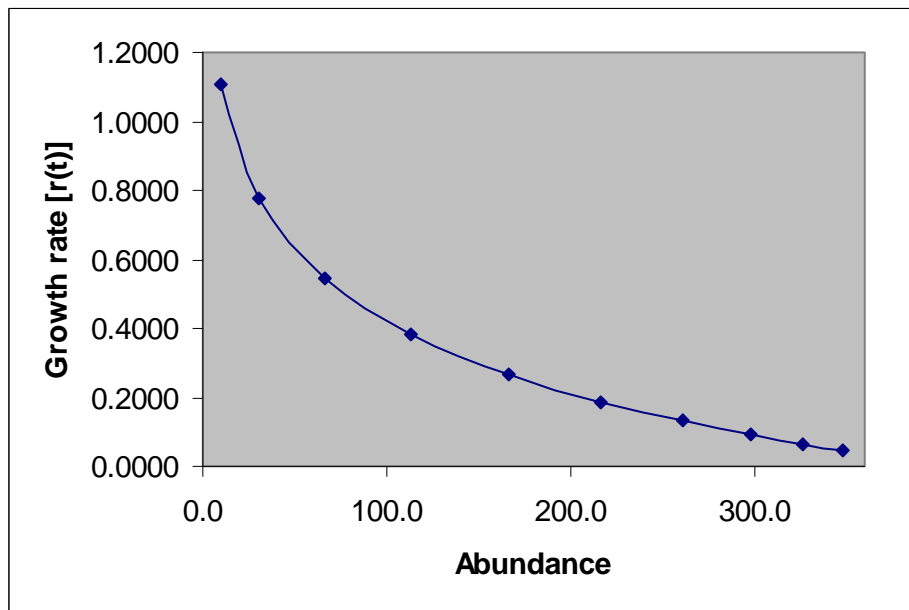
3. $\theta > 1$: Growth rate versus N is a convex relationship

A reminder on calculating geometric mean, and why λ_G is less than λ_A:

The geometric mean differs from the arithmetic mean because instead of adding a bunch of numbers and dividing by the total, you instead multiply a bunch of numbers (let's call it "t" numbers) and take the tth root of the product. To put these words into an equation for the geometric mean population growth rate (λ_G) over time:

$$\lambda_G = \sqrt[t]{(\lambda_1 * \lambda_2 * \lambda_3 * ... \lambda_t)}$$ or equivalently

$$\lambda_G = \left(\lambda_1 * \lambda_2 * \lambda_3 * ... \lambda_t \right)^{\frac{1}{t}}$$

The geometric mean will be less than the arithmetic mean when there is stochasticity. Let's run through an example. Suppose an endangered population grows at a constant $\lambda=1.05$; we would expect a 5% increase per year, so that in 16 years a population of 100 would have an expected size of

$$N_{16} = 100 * 1.05^{16} = 218$$

Now suppose instead that the population growth alternated each year between $\lambda = 1.55$ and $\lambda = 0.55$. The arithmetic mean of the growth rate is still 1.05 [from (1.55+0.55)/2]. But the growth of the average population is governed by the geometric mean which is

$$\sqrt{1.55 * 0.55} = 0.923.$$

After 16 years, the expected population size would be

$$N_{16} = 100 * 1.55^8 * 0.55^8 = 28.$$

This is the same as projecting all 16 years with the geometric mean: $100 * 0.923^{16} = 28$.

A population of 28 is a lot less than the 218 expected from the arithmetic mean! The variation in population growth leads to a likely decline for the population, even though the deterministic growth rate implies that the population should increase substantially.

An equivalent way to calculate the geometric mean population growth rate from a time series takes advantage of the mathematical properties of good old [$r=\ln(\lambda)$]:

1. Calculate r for each interval by $\ln(N_{t+1}/N_t)$.

2. Take the arithmetic mean of all of the r's to obtain $\bar{r}$.

3. Convert the $\bar{r}$ back to λ (by way of $\lambda = e^r$) and you've got your λ_G.

Another way to see the phenomenon (from Mills 2007):

Fig. 5.5 Stochastic geometric growth showing 25 possible population growth trajectories for hypothetical snail kite populations (e.g. Beissinger 1995) beginning with 10 individuals. For each replicate, λ at each of 20 time steps varied randomly between 0.5 and 1.7 ($\sigma_\lambda^2=0.12$). λ_A is therefore 1.1 and λ_G approximately 1.05 (represented by thick lines). Because λ_G represents median population growth, about half of the final abundances fall above the λ_G line and half below.

Computer Software

PopGrowthAnalysis

Visual Basic Program created by J. S. Horne, B. Dennis, J. Humbert, L. S. Mills, E. O. Garton.

- This program is a user-friendly 'front-end' to interface with the freely available program R (R Development Core Team 2006; program available online).

- Utilizes R contributed package *PopGrowth4*

- Input data can be a tab-delimited text file or a Microsoft Excel spreadsheet

- Allows user to fit several population growth models to time-series abundance data

  - Exponential growth with observation error (EGOE)

  - Exponential growth with process noise (EGPN)

  - Exponential growth state space (EGSS)

  - Ricker (logistic)-type density dependent growth

  - Gompertz density dependent growth

  - Theta-logistic density dependent growth

- Provides selection criteria (Akaike's Information Criteria) for EGPN, Ricker, Gompertz and Theta-logistic growth models

- Provides relevant parameter estimates and measures of precision of these estimates

- Enables user to easily implement *Viable Population Monitoring* (Staples et al. 2005) based on parameter estimates from EGPN and EGSS models

- Provides residuals from fitted models for investigating effects of environmental covariates and assessing correlations among populations

MetaPVA

Visual Basic Program in development by J. S. Horne, J. Tracey and E. O. Garton.

- Initiated (Before GRIP!) to allow users to easily implement several methods of sensitivity analysis

- Based on stochastic metapopulation projection model analogous to that used in RAMAS Metapop

- Utilizes R contributed package *Sensitivity*

- Currently allows more flexibility in how parameters are sampled and automates the sensitivity analysis

I. What is PVA? What does one look like?

Population viability analysis (PVA) comprises a set of analytical and modeling approaches for assessing the risk of extinction. It has been used to develop theory, to analyze population data and project trends, and to make policy decisions (Beissinger 2002). From its roots in early efforts to determine minimum viable population (MVP) sizes for imperiled species, PVA has developed into a powerful, quantitative tool for modeling population growth and persistence. The improvement in computational capabilities in recent years has allowed PVA to incorporate increasing complexity in population structures, processes, and spatial scales.

Computer simulation modeling, using either generic or customized computer programs, is the core of PVA.   On the basis of a set of demographic, life history, and environmental parameters specified by the user, the computer program creates a simulated population and steps it through annual cycles of reproduction and death until either extinction occurs or a specified time limit is reached. The program repeats this process for many simulated populations, and combines the results to produce estimates of the likelihood of specific outcomes. Simulation programs may be modified to include genetic factors, random environmental fluctuations, and catastrophic events, all of which are allowed to interact with one another. They can be used to predict effects of alternative scenarios on the population's genetic variability as well as its size. PVA is useful not only for predicting a population's fate or evaluating viable population sizes, but also for deciding how to use resources most efficiently in conservation efforts. By constructing "what-if" scenarios one can predict the impact of various potential management actions, and thus their cost effectiveness. PVAs have thus provided ecologists and managers with a framework for evaluating population declines and quantifying factors that threaten populations (Boyce 1992, Burgman et al. 1993, Brook et al. 2000, Akçakaya and Sjögren-Gulve 2000, Beissinger and McCullough 2002, Morris and Doak 2002).

Because habitat patchiness and landscape patterns have striking and long-lasting effects on population dynamics (Hanski and Gilpin 1991, Hanski 1998, Harrison and Bruna 1999, Lindenmayer et al. 2001), ecologists have added increasing spatial realism to their models. PVA models have expanded from a single-population focus to include multiple populations and explicit spatial structure (Lacy 1993, Lamberson et al. 1994, LeHaye et al. 1994, Dunning et al. 1995). One limitation of some metapopulation models is that they treat habitats as binary, with suitable patches surrounded by a matrix of unsuitable habitat types. In reality, matrix habitats are often capable of supporting some individuals, suggesting that models should treat landscapes as mosaics of patches of differing quality (Norton et al. 2000, Ricketts 2001). Another limitation is that although landscape changes through time strongly affect population dynamics (Fahrig 1992, Fahrig and Merriam 1994), most PVA models treat landscapes as unchanging.

Several PVA-based modeling approaches now offer more promising spatiotemporal analyses. For example, Akçakaya and colleagues are developing software that links transitional dynamics of the landscape with demographic models. Their software builds on the landscape succession model

LANDIS (Mladenoff et al. 1996) and the metapopulation package RAMAS GIS (Akçakaya 2000a). Changes in the landscape brought about by management actions and plant growth are summarized as a time series of habitat patches (Akçakaya 2001). Habitat-specific demography for the taxon of interest is then modeled for each time step based on observed demographic rates in different stand types. Demographic projections are therefore based on both local and landscape features. This combination is satisfying theoretically because it permits a variety of habitat patches that differ in quality and it allows habitat distribution and quality to change through time. In the context of management, this approach is also satisfying because many management actions require or cause continual changes in stand dynamics and landscape structure (e.g. managed fire, logging, and thinning: stand attributes change for decades following each perturbation).

Interpretation of PVA results is complicated by uncertainties inherent to modeling. Model performance, i.e. the likelihood of capturing observed dynamics or predicting dynamics accurately, is affected both by model structure (temporal and spatial detail) and by uncertainty in the data (Mills et al. 1996, Ludwig 1999, White 2000, Cross and Beissinger 2001). As more structural details are added to a model, the model becomes more realistic at the cost of decreased generality and increased parameter uncertainty. For example, as separate sets of vital rates (survival rates, fecundities, dispersal rates) are estimated for each age class or sex, and as populations are defined more locally, the realism of the model increases. But in some cases the additional parameters may actually reduce model performance because each parameter is estimated based on a smaller sample size, and hence may have higher uncertainty accruing from sampling error. The wise use of population models requires assessment of how model structure and data uncertainty affect model outcomes. In the case of species in fragmented landscapes, it is particularly important to know whether habitat-specific demographic information is required to produce reliable predictions. Modelers face three basic options when modeling a species living in a patchy landscape: (1) to ignore the spatial heterogeneity and treat the species of interest as one unified population, (2) to allow different demographic rates in different patch types, or (3) to allow both spatial and temporal landscape dynamics in which there are stand-specific demographic rates and stand distribution changes through time. The third approach is likely the most biologically realistic, but it is also much more data-hungry than are the first two approaches.

Population parameters such as birth rates and mortality rates vary through time and in different habitats (process variance). Even our best ecological methods provide us with estimates, not certainty, about these vital rates; the uncertainty associated with each estimate is sampling variance. Separating process and sampling variance can improve model performance (Gould and Nichols 1998, Morris and Doak 2002). Another data uncertainty problem arises when data are collected without model requirements in mind, which can result in a mismatch between model assumptions and data attributes. When data are insufficient for modeling, ecologists are forced to guess or to substitute parameter values from populations in other locations or even from other species. Because both sampling and process variance can bias risk assessment (Taylor 1995, Ludwig 1999, White 2000, Mills and Lindberg 2002), it is important to evaluate model reliability given data uncertainty.

PVA models can be used to produce comparative estimates, such as the relative increase in extinction risk due to different stressors. Such relative measures are less sensitive to uncertainties in the data than are absolute measures such as risk of extinction (Lindenmayer and Possingham 1996, Hanski 1997, Akçakaya and Raphael 1998). At present, PVA models are being widely used

to address risks to populations, but few of these models contain explicit or extensive analysis of the effects of model structure and data uncertainty on model results. That is problematic in the context of modeling to provide management information about threatened species, because it is not clear that the model outcomes truly reflect or predict population dynamics, rather than simply reflecting data uncertainty and model structure (Ludwig 1999, White 2000).

A number of approaches have been developed by various researchers to different levels of spatiotemporal complexity, uncertainty, management options. Commonly used modeling approaches include matrix models, diffusion analysis, Bayesian approaches, and individual-based models. Each type requires different data, and may answer different questions. Even within a particular class of PVA, each single-species model is unique, depending on the demographic characteristics, management issues, and amount of data available for that species.

We present here the mechanics and examples of two types of PVA that we will use for estimating extinction, recovery, and management impacts for listed species on DoD lands. Our analysis will focus on matrix models, which we have used extensively in our work, and individual-based models, which are promising methods for including spatial and demographic complexity.

II. Stochastic Matrix Models for PVA

A critical component of PVA is estimating the number of individuals N_t in a population at some time t in the future. Matrix models have long been used for estimating the most likely size of a population based on a straightforward relationship between age (or stage)-specific birth rates b and death rates d in a population and its future size (Leslie 1945). These models assume that individuals in a population can be categorized into $c = 0, 1, \ldots M$ discrete classes based on age, life history stages, sex, etc. Because many populations go through distinct birth pulses, matrix models treat time as a discrete process with intervals corresponding to the time between birth pulses, typically 1 year for vertebrates. Each class of individuals has a unique survival rate s_c and fecundity $F_c = s_c b_{c+1}$ during each time step. The survival rate is simply the proportion of individuals surviving from time t to $t+1$ and fecundity is the number of recruits per individual into the next time step.

In general, it is easy to see how the number of individuals n of class $c + 1$ at time $t + 1$ is

$$n_{c+1, t+1} = s_c n_{c,t} \qquad\qquad (1)$$

and the number of recruits is

$$n_{0,t+1} = \sum_{c=0}^{M} F_c n_{c,t} . \qquad\qquad (2)$$

We can combine equations 1 and 2 into a single equation using matrices. For example, if there are 4 classes of individuals,

$$\begin{bmatrix} n_0 \\ n_1 \\ n_2 \\ n_3 \end{bmatrix}(t+1) = \begin{bmatrix} F_0 & F_1 & F_2 & F_3 \\ s_0 & 0 & 0 & 0 \\ 0 & s_1 & 0 & 0 \\ 0 & 0 & s_2 & 0 \end{bmatrix}\begin{bmatrix} n_0 \\ n_1 \\ n_2 \\ n_3 \end{bmatrix}(t) \qquad (3)$$

Equation 3, known as the Leslie matrix population projection model, can be written more compactly using matrix and vector notation as $\mathbf{n}_{t+1} = \mathbf{Ln}_t$, where $\mathbf{L}$ is the population projection matrix.

A deterministic analysis of populations can be accomplished using the Leslie matrix projection model with temporally constant survival and fecundity. However, if vital rates (i.e., survival and fecundity) fluctuate under varying environmental conditions, it is important to incorporate this variability into population projections (Morris and Doak 2002, Caswell 2001). A stochastic matrix model can be formulated by assuming that vital rates arise from a multivariate distribution and that each projection matrix $\mathbf{L}$ at time t is a random draw from this distribution. A variety of distributions have been used to characterize vital rates with the most common being the beta distribution for survival rates and the gamma or lognormal distributions for fecundity rates (Fieberg and Ellner 2001), although uniform distributions are often used when data for estimating the mean and variance are limited.

Once a particular distribution has been decided for each vital rate, simulations can be used to calculate the long-term population trend over a sequence of time. Under the conditions of a stochastic matrix model outlined above, the log final population density at time t is approximately normally distributed with mean $\log(N_0) + \mu t$ and variance $\sigma^2 t$, where μ is the long-term stochastic growth rate of the population (Morris and Doak 2002). An estimate of μ can be obtained by projecting population growth over many (e.g., tens of thousands) time steps using projection matrices drawn at random from the specified distribution(s) at each time step. The estimate is calculated as

$$\log \hat{\mu} = \frac{1}{T-1} \sum_{t=1}^{T-1} \log[N(t+1)/N(t)] \qquad (4)$$

Estimates of $\log \mu$ can be used to determine whether a population is likely to grow or decline over the long term in a stochastic environment.

In addition to an estimate of the population trend, PVA is often interested in the probability that quasi-extinction (i.e., population falls below some critical size N_{EXT}) will occur prior to a specified time in the future. Again, this probability p_{EXT} can be estimated using simulations. If the population projection model is run for multiple realizations, then the fraction of realizations that the population size $\leq N_{EXT}$ during or before time t gives the probability of quasi-extinction.

The previous description outlines the basic structure of a stochastic matrix model for PVA. Depending on the particular species, environmental conditions, and available data, these models can be extended to account for density dependence (e.g. Mills et al. 1996, Ratner et al. 1997) correlations over time and among vital rates (Ferson and Burgman 1995), as well as metapopulation

dynamics (Hanski and Gilpin 1991, Hanski 1998, Harrison and Bruna 1999, Lindenmayer et al. 2001).

III. Individual-based Models for PVA

An alternative to stochastic matrix models that treat individuals as belonging to homogeneous classes with common vital rates are stochastic models that track the fates of individuals. By tracking each member of a population through space and time, individual-based models (IBMs) more easily accommodate key population characteristics such as demographic stochasticity, complex social structure, and unique life-history strategies. Additionally, by making the models spatially explicit, individual movements within a structured landscape can be incorporated. Because the structure of IBMs can be highly flexible, they tend to be tailored to specific species and systems. Thus, instead of describing a general model structure that could be used for any population, we provide a specific example of an IBM developed for the red-cockaded woodpecker in the southeastern United States (Letcher et al. 1998, Walters et al. 2002).

The IBM for red-cockaded woodpecker population dynamics was developed to incorporate the effects of complex social interactions and habitat fragmentation in population projections. Initial conditions for the model were set by specifying the number and spatial distribution of red-cockaded woodpecker territories on the landscape. Territories were then either left vacant or populated with either a breeding pair or a solitary male. The fates of these initial individuals, as well as any young produced, were followed for 100 years. Fates were determined by stochastic processes governing survival, dispersal, social status, and reproduction (Figure 1).

Individual females in the population occupied 1 of 3 age/social classes including: (1) fledgling – age <1 year (2) floater – nonbreeding adult in search of a territory with a solitary male (3) breeder – breeding adult occupying a territory with a male. Individual males in the population occupied 1 of 5 age/social classes including: (1) fledgling – age <1 year (2) floater – nonbreeding adult in search of an unoccupied territory (3) helper – nonbreeding adult assisting a breeding pair with the care of young (4) solitary – nonbreeding adult occupying a territory (5) breeder – breeding adult occupying a territory. Movements within the landscape and transitions between classes were dictated by random draws from appropriate probability distributions as well as the spatial arrangement and availability of occupied/unoccupied territories. Survival of individuals was a stochastic event dictated by unique survival probabilities for each age/social class. Reproduction of each breeding pair was a function of the male's age, the female's age, and the number of helpers in a territory.

With several replicate realizations, a mean annual population growth rate can be calculated using equation (4) as well as the percentage of original territories remaining after 100 years. These metrics then serve as the basis for investigating population viability under alternate scenarios of initial conditions (i.e., population size, distribution of territories, available habitat, etc.) and demographic rates (i.e., survival, reproduction, etc.).

IV. Comparison of Matrix Models and Individual-Based PVA

In general, IBM PVAs are most suited to species with complex life histories or those for which a great deal is known about their demography, individual behavior, and spatial use. For species with simpler life histories, or when data available for a species are less complete, life stage-based matrix models are more appropriate. Either approach could provide unbiased estimates of future population sizes under alternative management choices but our project will compare the success of each approach when applied in an ex post facto analysis to real species for which management actions were taken. We will use this analysis to examine the performance of each approach and explore their potential for evaluating consequences of management alternatives for listed species occurring on DoD facilities.

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PopGrowth_beta: Installation and Tutorial

PopGrowth_beta.exe is a program written in Visual Basic 6. It is a "front-end" user-friendly interface for analyzing time-series data common to ecological investigations.

When running PopGrowth_beta.exe, the free statistical computing software R (http://cran.r-project.org/) and R contributed package *PopGrowth4* is used for many of the calculations. This is done in the background and users do not need to be familiar with R to use PopGrowth_beta.exe.

For programs written in Visual Basic (e.g., PopGrowth) to be able to open and communicate with R, an "R-(D)COM server" needs to be installed.

> *"R-(D)COM is a programmation interface to COM and DCOM (ex ActiveX; Microsoft distributed object interface) to access the R calculation engine. As such, it runs only under the Windows environment. The R-(D)COM server can be used to build a R GUI client using tools like Microsoft C++, Microsoft Visual Basic, or Microsoft Excel. Currently, a R-Excel addin is provided, as well as some examples to use Visual Basic as a frontend."* (From http://www.sciviews.org/_rgui/projects/RDcom.html)

Steps to install PopGrowth_beta.exe

1. Make sure R is installed on the computer. If not you can download an installation program free from (http://cran.r-project.org/). The program was written with version 2.6.1 and has not been tested with other versions.

2. Install the R contributed package "PopGrowth4" by putting the folder "PopGrowth4" in the "C:/ProgramFiles/R/R-2.6.1/library" folder. See the 'Packages' link at http://cran.r-project.org/ to learn more about R contributed packages.

3. Make sure the R – (D)COM server is installed. There will be a folder called '(D)COM Server' in "C:/ProgramFiles/R/" if installed. If not already installed, run *RSrv250.exe*

   > **Note: R – (D)COM comes with an addin that allows communication between Microsoft Excel and R. This is **NOT** needed to run PopGrowth_beta.exe. It has been my experience that installing this addin does strange things when Microsoft Excel is opened. To avoid this, **do not select the check boxes for "RExcel:Excel Add-In" or "RExcel Sample Files"**

4. Lastly, make sure there is a file 'MSHFLXGD.OCX' in 'System32' windows folder. This file comes with many software programs but if it is not in your 'System32' windows folder, put it there and register it. There are several ways to register a *.ocx file. I found the following worked…

   a. Get a command prompt. Go to 'Start > Programs > Accessories > Command Prompt'

   ** Note if you are running Windows Vista, right click on 'Command Prompt' and select 'Run as administrator'**

   b. Navigate to the 'System32' directory using the command 'cd'. To go up in the directory, type 'cd..' until you get to 'C:\'. Then type 'cd windows' and press Enter. Then type 'cd system32' and press Enter. The command prompt should read 'C:\Windows\System32>'

   c. Type 'regsvr32 mshflxgd.ocx'. You should receive a message confirming… 'DllRegisterServer in mshflxgd.ocs succeeded'.

5. Place the file PopGrowth_beta.exe where you want the program to be opened from and double-click to run the program.

OPENING AND LOADING INPUT DATA

Open an input file by choosing *File > Open*

The input file can be a tab-delimited text file or a Microsoft Excel Workbook. Two of the columns of data should correspond to time and abundance.

If the selected file is a Microsoft Excel Workbook, load the data by clicking on the appropriate worksheet name.

You can change the y-axis (abundance) or the x-axis (time) by selecting the appropriate column and clicking the "Apply current selection…" button.

ANALYSIS OPTIONS

PopGrowth contains two main analysis options including: (1) Fitting various growth models to the time series of abundance data and (2) Viable population monitoring.

A. Fitting Growth Models

PopGrowth fits 3 stochastic population growth models without density dependence:
1. Exponential growth with observation error
2. Exponential growth with process noise
3. Exponential growth with observation error and process noise (State Space)

PopGrowth fits 3 stochastic population growth models incorporating density dependence:
4. Ricker
5. Gompertz
6. Theta-logistic

These models are described in more detail under **OUTPUT** section.

To fit any of these models select *Analyses > Fit Growth Model(s)*

Select the appropriate check boxes next to the models you wish to fit then click *Next >>*.

- Parameter estimates and each models' Akaike Information Criteria can be saved to a text file using *Output > Save text output*

- If one of the density dependent models is selected an additional input form will appear asking for parameters related to confidence intervals calculated using parametric bootstrap

For exploratory analyses, 300 bootstrap replicates is sufficient and quite a bit faster.

B. Viable Population Monitoring

Viable population monitoring is a risk based monitoring strategy described by Staples et al. 004 (Conservation Biology 19:1908 -1916). It estimates probability of "quasi-extinction" through time.

To calculate these probabilities, select *Analyses > Viable Population Monitoring*

You will need to specify 3 parameters:

1. The lower threshold population size. This is the quasi-extinction threshold.

2. The time in the future for which the probability of reaching the threshold applies. The output probabilities will be the "probability that the population will reach or fall below the threshold within the specified time in the future.

3. Model parameters (which determine the probability of extinction) are estimated with each additional data point in the time series. You will need to specify the amount of time since the first observation to begin calculating these parameters and estimating the probability of reaching the threshold. For example, with a data set that is 20 years in length, if you specify 10, then the parameters will be estimated with the first 10 years of data and a probability of reaching the threshold will be calculated. The next probability is calculated by estimating parameters with the first 11 years of data, then the first 12 years of data, and so on.

The probability of extinction is based, in part, on the estimate of process variance. This estimate can be obtained using either the exponential growth model with process noise only (EGPE) or the exponential growth model with process noise and observation error (EGSS).

For certain parameter estimates, an approximation needs to be implemented to calculate the probability of extinction. This is not necessarily a problem but the program alerts the user of this. This may happen several times during the calculations. Just select *OK* each time the message box appears.

Graphical output is displayed on the Main form. Text output of Viable Population Monitoring (for making your own plots) can be save by *Output > Save text output*

OUTPUT

All output is saved as a tab-delimited text file. Values from these text files can be cut and pasted into Excel.

Output will contain:

1. The input data

2. Akaike's Information Criteria corrected for small sample bias (AICc) for the EGPE, Ricker, Gompertz, and theta-logistic models. AICc values are not comparable for the EGOE and EGSS models.

3. Estimated model parameters

   a. Exponential growth with observation error (EGOE): 3 parameters N_0, μ and τ

   $$\ln(N_t) = \ln(N_0) + \mu t + F$$

   where, $F \sim normal(0, \tau^2)$; N_0 is the estimated initial abundance; μ is the trend; τ^2 is the "sampling variance" due to observation error.

   b. Exponential growth with process noise (EGPE): 2 parameters μ and σ

   $$d \ln N(t) = \mu\, dt + dB(t)$$

   where, $dB(t) \sim normal(0, \sigma^2 dt)$; σ^2 is the "process variance" related due to environmental variation in population growth rates

   c. Exponential growth with process noise and observation error (EGSS): 4 parameters N_0, μ, σ, and τ

   $$d \ln N(t) = \mu dt + dB(t),$$ unobserved stochastic population growth

   $$Y(t) = \ln N(t) + F_i$$ observed   abundance

d. Ricker: 3 parameters a, b, and σ

$$\ln\left(N_{t+1}/N_t\right) = a + bN_t + E$$

where, $E \sim normal\left(0, \sigma^2\right)$

e. Gompertz: 3 parameters a, b, and σ

$$\ln\left(N_{t+1}/N_t\right) = a + b \times \ln\left(N_t\right) + E$$

f. Theta-logistic: 4 parameters a, b, θ and σ

$$\ln\left(N_{t+1}/N_t\right) = a + bN_t^{\theta} + E$$

4. Residuals for models EGPE, Ricker and Gompertz. These can be used to identify correlations among populations in a metapopulation or investigate possible influences of environmental covariates on growth rates.

Example output from fitting all models to data "Wolf2.xls"

Data:

Time Abundance
1989 4.91
1990 2.47
1991 2.8
1992 3.62
1993 2.53
1994 2.23
1995 2.82
1996 2.75
1997 2.33
1998 3.04
1999 1.59
2000 1.2
===
Information Theoretic Model Selection (Akaike's Information Criteria)

Model	AICc
EGPE	12.074
Ricker	10.97
Gompertz 12.407	
Theta-L	15.395

===

Model fit of exponential growth with observation error

Parameter	estimate	Standard	Error
Init_abund	3.7775785048		
Trend (mu)	-0.0720465574	0.0218640798	
Sampling variance	0.068359432		
Process variance	NA: assumed = 0		

===

Model fit of exponential growth with process noise

Parameter	estimate	Standard	Error
Init_abund	4.91		
Trend (mu)	-0.1280865805	0.1031663266	
Sampling variance	NA: assumed = 0		
Process variance	0.1170762003		

===

Model fit of exponential growth with observation error and process noise
----

Parameter	estimate	Standard	Error
Init_abund(ML)	3.7775327569		
Trend [mu(ML)]	-0.0720449931		
Sampling variance (ML)	0.056968608		
Process variance (ML)	0.0000000001		

Init_abund(REML)	4.0285257157		
Trend [mu(REML)]	-0.0953790647	0.056132318	
Sampling variance(REML)	0.0439179546		
Process variance(REML)	0.0295019512		

===

Model fit of Ricker density dependent growth with process noise
----

P	arameter estimate	95%	Lower C.I.	95% Upper C.I.
a_hat	0.5545029297		0.2093225381	1.0808208086
b_hat	-0.2415080287		-0.4306277829	-0.1209474678
sigma_hat	0.2595369277		0.1369360956	0.3526803471
==

Model fit of Gompertz density dependent growth with process noise
----

P	arameter estimate	95%	Lower C.I.	95% Upper C.I.
a_hat	0.5068333776		0.1816265227	1.046157398
b_hat	-0.6342508799		-1.1703701546	-0.3225267201
sigma_hat	0.2770553233		0.1457821309	0.3498999459
==

Model fit of Theta-logistic density dependent growth with process noise
----

P	arameter estimate
a_hat	0.1159992976
b_hat	0.014549738
theta_hat	2.557183594
sigma_hat	0.2501186494
==

Residuals from EGPE fit

Time Abundance	ln(Abund)	ln[Lambda(t)]	Residuals
1989 4.91	1.59127394180643	-0.687055791166543	-0.558969210710864
1990 2.47	0.904218150639886	0.125401266541272	0.253487846996952
1991 2.8	1.02961941718116	0.256854608656521	0.384941189112201
1992 3.62	1.28647402583768	-0.358254723098251	-0.230168142642571
1993 2.53	0.928219302739429	-0.126217717267401	1.86886318827809E-03
1994 2.23	0.802001585472027	0.234735299477995	0.362821879933674
1995 2.82	1.03673688495002	-2.51359732715423E-02	0.102950607184137
1996 2.75	1.01160091167848	-0.165732644100871	-3.76460636451912E-02
1997 2.33	0.845868267577609	0.265989247840521	0.394075828296201
1998 3.04	1.11185751541813	-0.64812349918599	-0.520036918730311
1999 1.59	0.46373401623214	-0.281412459438186	-0.153325878982506
2000 1.2	0.182321556793955		

Residuals from Ricker fit

Time Abundance	ln(Abund)	ln[Lambda(t)]	Residuals
1989 4.91	1.59127394180643	-0.687055791166543	-5.57543000175069E-02
1990 2.47	0.904218150639886	0.125401266541272	0.16742316768116
1991 2.8	1.02961941718116	0.256854608656521	0.378574159264859
1992 3.62	1.28647402583768	-0.358254723098251	-3.84985889622483E-02
1993 2.53	0.928219302739429	-0.126217717267401	-6.97053344059778E-02
1994 2.23	0.802001585472027	0.234735299477995	0.218795273731736
1995 2.82	1.03673688495002	-2.51359732715423E-02	0.101413737910641
1996 2.75	1.01160091167848	-0.165732644100871	-5.60884949271466E-02
1997 2.33	0.845868267577609	0.265989247840521	0.27420002496349
1998 3.04	1.11185751541813	-0.64812349918599	-0.468442021691507
1999 1.59	0.46373401623214	-0.281412459438186	-0.451917623547499
2000 1.2	0.182321556793955		

Residuals from Gompertz fit

Time	Abundance	ln(Abund)	ln[Lambda(t)]	Residuals
1989	4.91	1.59127394180643	-0.687055791166543	-0.184622270984678
1990	2.47	0.904218150639886	0.125401266541272	0.19206904661337
1991	2.8	1.02961941718116	0.256854608656521	0.403058252377011
1992	3.62	1.28647402583768	-0.358254723098251	-4.91408178227695E-02
1993	2.53	0.928219302739429	-0.126217717267401	-4.43271853567864E-02
1994	2.23	0.802001585472027	0.234735299477995	0.23657213314875
1995	2.82	1.03673688495002	-2.51359732715423E-02	0.125581930644237
1996	2.75	1.01160091167848	-0.165732644100871	-3.09572533505152E-02
1997	2.33	0.845868267577609	0.265989247840521	0.29564856323644
1998	3.04	1.11185751541813	-0.64812349918599	-0.449760269294766
1999	1.59	0.46373401623214	-0.281412459438186	-0.494122129210293
2000	1.2	0.182321556793955		

Example output from Viable Population Monitoring with data "Bear2.xls"

Data:

Time Abundance
1959 44
1960 47
1961 46
1962 44
.
.
.
1997 99
==

Information Theoretic Model Selection (Akaike's Information Criteria)

Model   AICc
==

Viable Population Monitoring (VPM)

Probability of reaching population size of 30 within a time period of 50

Time Abundance	mu(EGPN)	variance(EGPN)	Probability(EGPN)	mu(EGSS)	variance(EGSS)	Probability (EGSS)
1959 44						
1960 47						
1961 46						
1962 44						
1963 46						
1964 45						
1965 46						
1966 40						
1967 39						
1968 39						
1969 42						
1970 39						
1971 41						
1972 40						
1973 33						
1974 36						
1975 34						
1976 39						
1977 35						
1978 34						
1979 38	-0.00733	0.00708	0.840179	-0.015024	0	1
1980 36	-0.009556	0.00683	0.908833	-0.01364	0.000157	1
1981 37	-0.007876	0.006567	0.867629	-0.011427	0.000532	0.993539
1982 41	-0.00307	0.006799	0.673913	-0.007067	0.001384	0.700152
1983 39	-0.005026	0.006596	0.769062	-0.006511	0.001436	0.745598
1984 51	0.005905	0.009308	0.299205	0.001713	0.003581	0.160794
1985 47	0.002537	0.009231	0.44658	0.001826	0.003458	0.21819
1986 57	0.009587	0.010218	0.18133	0.007211	0.004561	0.054431
1987 48	0.003108	0.011015	0.457287	0.003863	0.003862	0.16886
1988 60	0.010695	0.012291	0.184336	0.008067	0.0041	0.024796
1989 65	0.013007	0.012028	0.115301	0.011319	0.004746	0.011377
1990 74	0.01677	0.012066	0.050444	0.015218	0.00566	0.003957
1991 69	0.01406	0.011912	0.083924	0.014103	0.005278	0.006062
1992 65	0.011824	0.011705	0.122378	0.012194	0.005196	0.013263

1993	57	0.007614	0.011953		0.255309		0.008472	0.00587		0.078479
1994	70	0.013266	0.012719	0.098905			0.011676	0.005265	0.009725	
1995	81	0.016952	0.012845	0.04191			0.015378	0.006059	0.002893	
1996	99	0.021917	0.0134	0.011682	0.020667			0.008302		0.001326
1997	99	0.02134	0.013051	0.011382			0.021091	0.008222	0.001132	

===

PRESENTATIONS

Population Viability Analysis and Population Growth Models: An Overview

Population Viability Analysis
and
Population Growth Models:
An Overview

1

Population Viability Analysis

Application of data and models to estimate probabilities that a population will persist for specified times into the future (Mills 2007)

2

Population Viability Analysis

Application of data and models to estimate probabilities that a population will persist for specified times into the future (Mills 2007)

3

Population Viability Analysis

1. Count-based (based on time series of abundance)

2. Demographically explicit (based on vital rates)

4

Count-based PVA

- Census of the entire population

- Index representing a subset of the population (e.g., breeding pairs, flowering plants, lek counts)

- Estimated over multiple (not necessarily consecutive) years

5

Count-based PVA

Population growth models:

- Density-independent (in unlimited environments)

- Density- dependent (in limited environments)

➢ Using the appropriate population growth model is critical to projecting future growth and viability

6

Population Projection
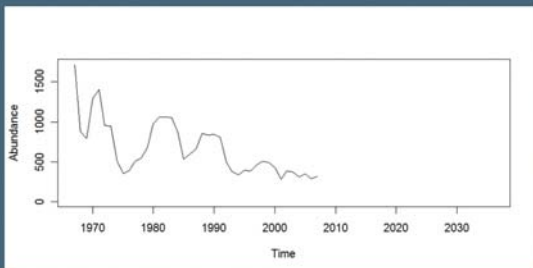
Population Projection
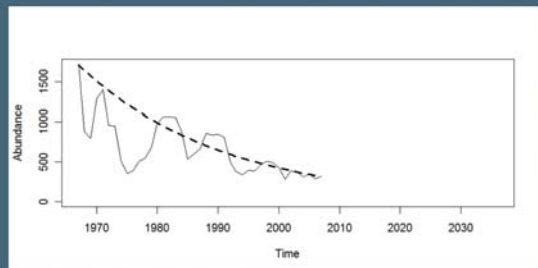
Population Projection
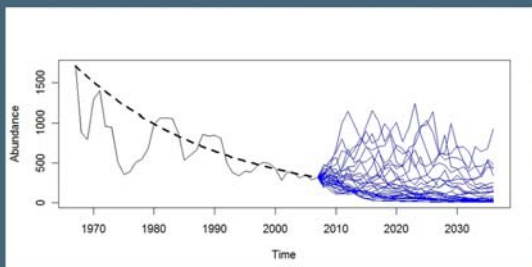
Population Persistence
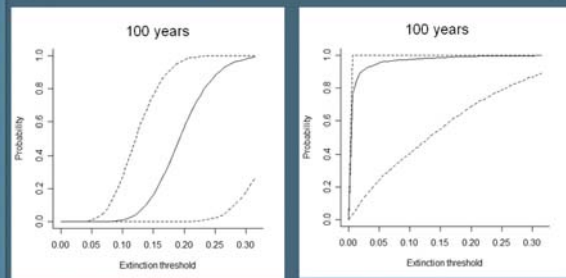
Gompertz density-dependent model   Exponential model with process noise

Population Growth Models

- Deterministic exponential growth model: for discrete geometric population growth

$$N_{t+1}=\lambda_t N_t$$

- Assumes that population growth is density independent (i.e. is not affected by population size, N_t)

$N_{t+1}=\lambda_t N_t$

If there is no variation in the environment from year to year, then the population growth rate λ will be constant, and only three types of population growth are possible

$\lambda>1$
Geometric increase

Stable $\lambda=1$

Geometric decline $\lambda<1$
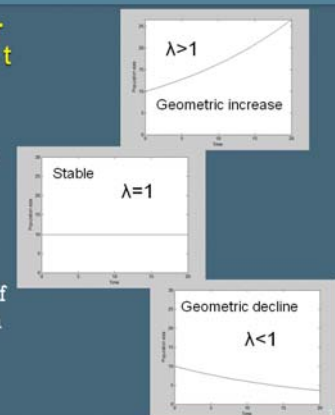
Population Growth in a Randomly Varying Environment

Environmental variability will cause the population growth rate (λ) to vary by causing survival and reproduction to vary from year to year

Change in population size over time is a stochastic process

The best we can do is talk about *probabilities*

13

A key point about environmental stochasticity:

Adding variation to population growth means:

- population growth is more variable, AND
- populations generally grow more slowly over the long term than with constant growth rate

14

Geometric mean growth rate: λ_G

λ_G is the best predictor of whether N_t will increase or decrease over the long term

λ_G will be less than the arithmetic mean (λ_A) when there is stochasticity

λ_G is defined as

$$\lambda_G = (\lambda_t \, \lambda_{t-1} \, \lambda_{t-2} \, \ldots \lambda_1 \, \lambda_0)^{(1/t)}$$

15

Converting λ_G to the log scale

$$\mu = \ln\lambda_G = \frac{\ln\lambda_t + \ln\lambda_{t-1} + \ldots \ln\lambda_1 + \ln\lambda_0}{t}$$

μ is the measure of stochastic population growth on a log scale

If $\mu > 0$, then $\lambda > 1$ » most populations will grow

If $\mu < 0$, then $\lambda < 1$ » most populations will decline

16

Two important parameters for exponential growth:

- μ : tells us the direction in which the population will tend to move over time

- σ^2 (= variance in the log population growth rate):
  - greater with more variation in growth rate from year to year
  - greater σ^2 => greater range of possible population sizes in the future

17

Stochastic Exponential Growth Models

1. Exponential growth with observation error (EGOE)

   -- Stochasticity arises only from imprecision of abundance estimates

18

Stochastic Exponential Growth Models

1. Exponential growth with observation error (EGOE)

μ = slope => population trend
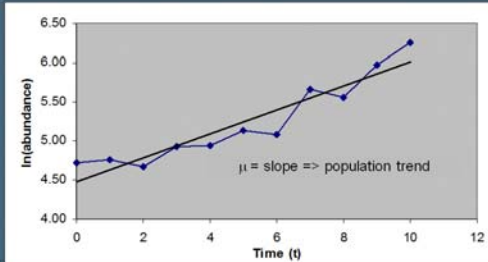
Stochastic Exponential Growth Models

2. Exponential growth with process noise (EGPN)

-- Process noise: environmental stochasticity bumps the population growth around

Stochastic Exponential Growth Models

3. Exponential growth state space

-- Stochasticity arises from both process noise and observation error

Density-dependent Population Growth

- Limited environments cause birth and/or vital rates to decline with increasing population size

- Intraspecific competition causes growth rates to decline with increasing population size

Population Growth Models with Density Dependence

1. Stochastic logistic (Ricker) growth model

- Growth rate is a decreasing linear function of population size

- Important parameters:

  1. a = maximum growth rate at N = 0

  2. b = effect of intraspecific competition

Population Growth Models with Density Dependence

1. Stochastic logistic (Ricker) growth model
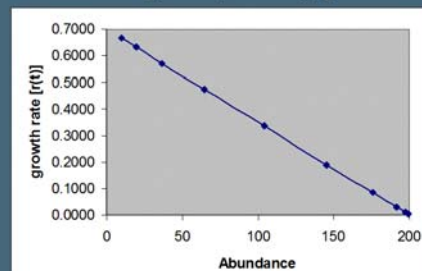
2. Stochastic Gompertz growth model

- Growth rate is a decreasing linear function of the natural log of population size

---
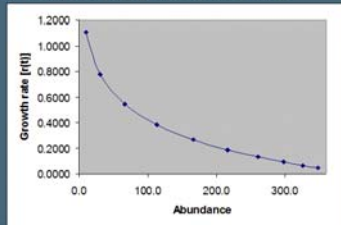
Population Growth Models with Density Dependence

3. Stochastic theta-logistic growth model

- Growth rate is a decreasing linear function of population size raised to the power theta (θ)

Finding the "best" model

- Information-theoretic approach to model selection
  - we use Akaike's Information Criterion (AIC) to evaluate models

- Support is higher for
  - models with higher likelihoods, and
  - models with fewer parameters

Estimating Probability of Persistence

- Fit a number of models
- Select the best model
- Use parameter estimates from best model to project future growth

PopGrowth:
Software for Fitting Population Growth Models to Time Series Abundance Data

Analysis Options

1. Fit Stochastic Growth Models

2. Implement Viable Population Monitoring

Population Growth Models

1. Density Independent Growth Models
   - Exponential growth with observation error
   - Exponential growth with process noise
   - Exponential growth with process noise and observation error
2. Density Dependent Growth Models
   - Ricker
   - Gompertz
   - Theta-logistic

Density Independent Growth Models

- Exponential Growth with Observation Error

$$\ln\left(N_t\right) \sim normal\left(\ln\left(N_0\right) + \mu t, \tau^2\right) \rightarrow \text{"Trend"}$$

- Exponential Growth with Process Noise
  (Dennis et al. 1991)

$$\ln\left(N_{t+1}/N_t\right) \sim normal\left(\mu, \sigma^2\right)$$

- Exponential Growth with both sources of variation
  ('State-space model of Staples et al. 2004)

Density Dependent Growth Models

- Ricker

$$\ln\left(N_{t+1}/N_t\right) \sim normal\left(a + bN_t, \sigma^2\right)$$

- Gompertz

$$\ln\left(N_{t+1}/N_t\right) \sim normal\left(a + b * \ln\left(N_t\right), \sigma^2\right)$$

- Theta-logistic

$$\ln\left(N_{t+1}/N_t\right) \sim normal\left(a + b\left(N_t\right)^\theta, \sigma^2\right)$$

Model Fit
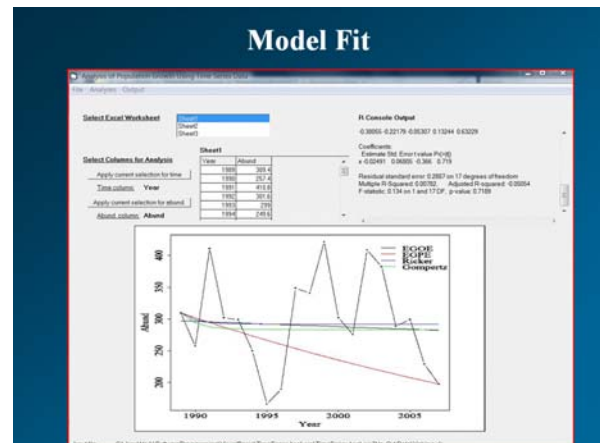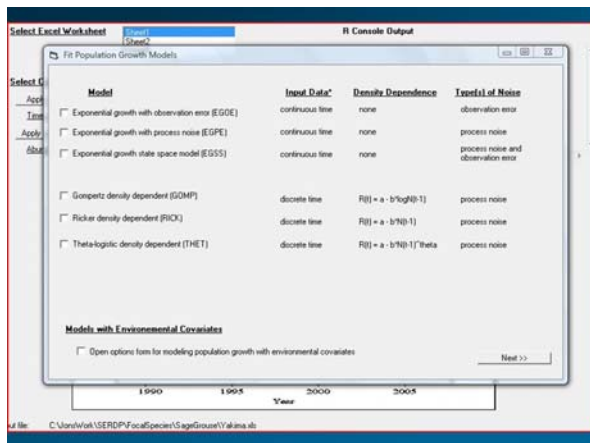
Graphics Output
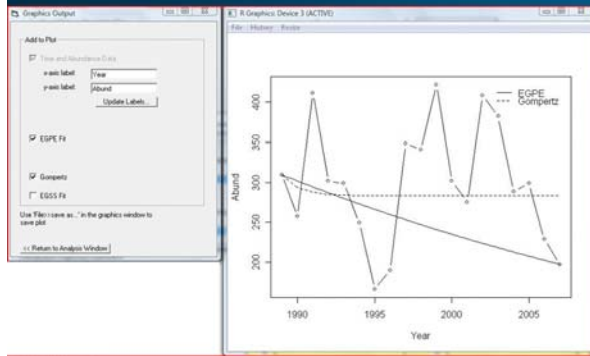
Text Output

- Input Data

- Akaike Information Criteria
  - EGPE, Ricker, Gompertz, Theta-logistic

- Parameter Estimates (Std. Error or Confidence Intervals)

- Residuals
  - EGPE, Ricker, Gompertz

Viable Population Monitoring

- Risk-based monitoring strategy[1]

  - Estimates probability of "quasi"-extinction through time

  - can detect changes in "extinction" risk before trend estimates are significant

  - PopGrowth provides easy way to implement VPM for annual evaluation of risk

[1] Staples et al. 2004. Risk-based population monitoring. Conservation Biology

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Viable Population Monitoring

Application to Sage Grouse
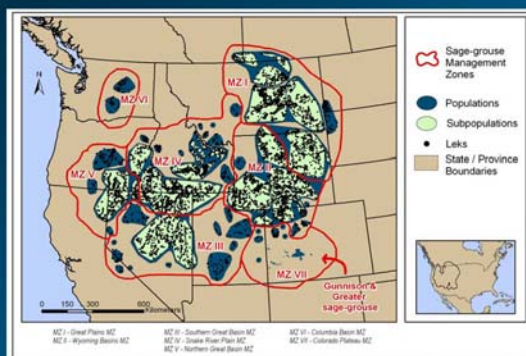
Grouse Management Zone 6

- Parameter Estimates

	Parameters			AICc
	a	b	σ^2	
EGPE	-0.051		0.060	4.00
Gompertz	0.875	-0.141	0.052	1.52

Probability of Extinction
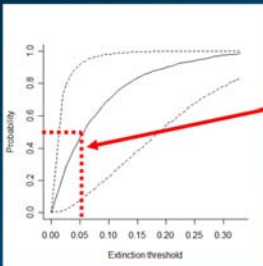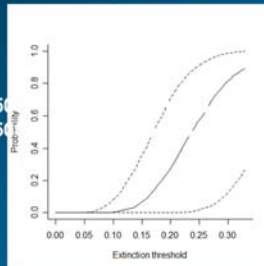
VIABLE POPULATION MONITORING
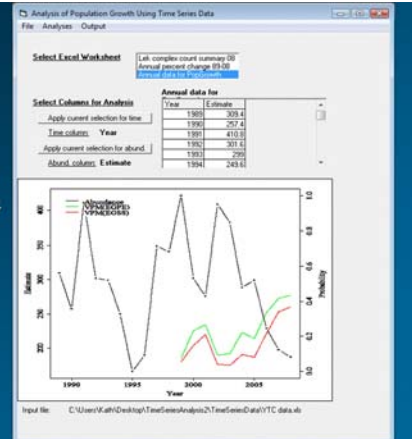
Uses of PopGrowth

- Select best model given the data

- Use parameter estimates to determine: trend, probability of persistence, density dependence...

- Evaluate residuals for correlations among populations and effects of environmental covariates

- Viable Population Monitoring

Appendix E. Other Supporting Material

PopGrowth_beta: Installation and Tutorial

The most recent version of PopGrowth can be downloaded from:
http://www.cnr.uidaho.edu/population_ecology/

PopGrowth_beta.exe is a program written in Visual Basic 6. It is a "front-end" user-friendly interface for analyzing time-series data common to ecological investigations.

When running PopGrowth_beta.exe, the free statistical computing software R (http://cran.r-project.org/) and R contributed package *PopGrowth4* are used for many of the calculations. This is done in the background and users do not need to be familiar with R to use PopGrowth_beta.exe.

For programs written in Visual Basic (e.g., PopGrowth) to be able to open and communicate with R, an "R-(D)COM server" needs to be installed.

"R-(D)COM is a programmation interface to COM and DCOM (ex ActiveX; Microsoft distributed object interface) to access the R calculation engine. As such, it runs only under the Windows environment. The R-(D)COM server can be used to build a R GUI client using tools like Microsoft C++, Microsoft Visual Basic, or Microsoft Excel. Currently, a R-Excel addin is provided, as well as some examples to use Visual Basic as a frontend." (From http://www.sciviews.org/_rgui/projects/RDcom.html)

Steps to install PopGrowth_beta.exe

1.) Make sure R is installed on the computer. If not, you can download an installation program free from (http://cran.r-project.org/). The program was written with version 2.6.1 and has not been tested with other versions. It will not work with version 2.8 or greater.

2.) Install the R contributed package "PopGrowth4" by putting the folder "PopGrowth4" in the "C:/ProgramFiles/R/R-2.6.1/library" folder. See the 'Packages' link at http://cran.r-project.org/ to learn more about R contributed packages.

3.) Make sure the R – (D)COM server is installed. There will be a folder called '(D)COM Server' in "C:/ProgramFiles/R/" if installed. If not already installed, run *RSrv250.exe*

Note: R – (D)COM comes with an addin that allows communication between Microsoft Excel and R. This is **NOT needed to run PopGrowth_beta.exe. It has been my experience that

installing this addin does strange things when Microsoft Excel is opened. To avoid this, **do not select the check boxes for "RExcel:Excel Add-In" or "RExcel Sample Files"**

4.) Lastly, make sure there is a file 'MSHFLXGD.OCX' in 'System32' windows folder. This file comes with many software programs but if it is not in your 'System32' windows folder, put it there and register it. There are several ways to register a *.ocx file. I found the following worked…

    a. Get a command prompt. Go to 'Start > Programs > Accessories > Command Prompt'
    b. ** Note if you are running Windows Vista, right click on 'Command Prompt' and select 'Run as administrator'**
    c. Navigate to the 'System32' directory using the command 'cd'. To go up in the directory, type 'cd..' until you get to 'C:\'. Then type 'cd windows' and press Enter. Then type 'cd system32' and press Enter. The command prompt should read 'C:\Windows\System32>'
    d. Type 'regsvr32 mshflxgd.ocx'. You should receive a message confirming… 'DllRegisterServer in mshflxgd.ocs succeeded'.
    e. Vista users: If the registration does not succeed, you might try restarting you computer and repeat steps 2 and 3.

5.) Place the file PopGrowth_beta.exe where you want the program to be opened from and double-click to run the program.

OPENING AND LOADING INPUT DATA

Open an input file by choosing *File > Open*

The input file can be a tab-delimited text file or a Microsoft Excel Workbook. Two of the columns of data should correspond to time and abundance. For this version, there should be no missing values in the data.

If the selected file is a Microsoft Excel Workbook, load the data by clicking on the appropriate worksheet name.

You can change the y-axis (abundance) or the x-axis (time) by selecting the appropriate column and clicking the "Apply current selection…" button.

ANALYSIS OPTIONS

PopGrowth contains two main analysis options including: (1) Fitting various growth models to the time series of abundance data and (2) Viable population monitoring.

A. Fitting Growth Models

PopGrowth fits 3 stochastic population growth models without density dependence:
1. Exponential growth with observation error
2. Exponential growth with process noise
3. Exponential growth with observation error and process noise (State Space)

PopGrowth fits 3 stochastic population growth models incorporating density dependence:
4. Ricker
5. Gompertz
6. Theta-logistic

These models are described in more detail under **OUTPUT** section.

To fit any of these models select *Analyses > Fit Growth Model(s)*
Select the appropriate check boxes next to the models you wish to fit then click *Next >>*.

- Parameter estimates and each models' Akaike Information Criteria can be saved to a text file using *Output > Save text output*

- If one of the density dependent models is selected an additional input form will appear asking for parameters related to confidence intervals calculated using parametric bootstrap

For exploratory analyses, 300 bootstrap replicates is sufficient and quite a bit faster.

B. Viable Population Monitoring

Viable population monitoring is a risk based monitoring strategy described by Staples et al. 2004 (Conservation Biology 19:1908 -1916). It estimates probability of "quasi-extinction" through time.

To calculate these probabilities, select *Analyses > Viable Population Monitoring*

You will need to specify 3 parameters:

1. The lower threshold population size. This is the quasi-extinction threshold.

2. The time in the future for which the probability of reaching the threshold applies. The output probabilities will be the "probability that the population will reach or fall below the threshold within the specified time in the future.

3. Model parameters (which determine the probability of extinction) are estimated with each additional data point in the time series. You will need to specify the amount of time since the first observation to begin calculating these parameters and estimating the probability of reaching the threshold. For example, with a data set that is 20 years in length, if you specify 10, then the parameters will be estimated with the first 10 years of data and a probability of reaching the threshold will be calculated. The next probability is calculated by estimating parameters with the first 11 years of data, then the first 12 years of data, and so on.

The probability of extinction is based, in part, on the estimate of process variance. This estimate can be obtained using either the exponential growth model with process noise only (EGPE) or the exponential growth model with process noise and observation error (EGSS).

For certain parameter estimates, an approximation needs to be implemented to calculate the probability of extinction. This is not necessarily a problem but the program alerts the user of this. This may happen several times during the calculations. Just select *OK* each time the message box appears.

Graphical output is displayed on the Main form. Text output of Viable Population Monitoring (for making your own plots) can be save by *Output > Save text output*

OUTPUT

All output is saved as a tab-delimited text file. Values from these text files can be cut and pasted into Excel.

Output will contain:

1. The input data

2. Akaike's Information Criteria corrected for small sample bias (AICc) for the EGPE, Ricker, Gompertz, and theta-logistic models. AICc values are not comparable for the EGOE and EGSS models.

3. Estimated model parameters

   a. Exponential growth with observation error (EGOE): 3 parameters N_0, μ and τ

   $$\ln(N_t) = \ln(N_0) + \mu t + F$$

   where, $F \sim normal(0, \tau^2)$; N_0 is the estimated initial abundance; μ is the trend; τ^2 is the "sampling variance" due to observation error.

   b. Exponential growth with process noise (EGPE): 2 parameters μ and σ

   $$d \ln N(t) = \mu \, dt + dB(t)$$

   where, $dB(t) \sim normal(0, \sigma^2 dt)$; σ^2 is the "process variance" related due to environmental variation in population growth rates

   c. Exponential growth with process noise and observation error (EGSS): 4 parameters N_0, μ, σ, and τ

   $$d \ln N(t) = \mu dt + dB(t),\qquad \text{unobserved stochastic population growth}$$
   $$Y(t) = \ln N(t) + F \qquad\qquad \text{observed abundance}$$

d. Ricker: 3 parameters a, b, and σ

$$\ln\left(N_{t+1}/N_t\right) = a + bN_t + E$$

where, $E \sim normal\left(0, \sigma^2\right)$

e. Gompertz: 3 parameters a, b, and σ

$$\ln\left(N_{t+1}/N_t\right) = a + b \times \ln\left(N_t\right) + E$$

f. Theta-logistic: 4 parameters a, b, θ and σ

$$\ln\left(N_{t+1}/N_t\right) = a + bN_t^{\theta} + E$$

4. Residuals for models EGPE, Ricker and Gompertz. These can be used to identify correlations among populations in a metapopulation or investigate possible influences of environmental covariates on growth rates.

Example output from fitting all models to data "Wolf2.xls"

Data:

Time	Abundance
1989	4.91
1990	2.47
1991	2.8
1992	3.62
1993	2.53
1994	2.23
1995	2.82
1996	2.75
1997	2.33
1998	3.04
1999	1.59
2000	1.2

==

Information Theoretic Model Selection (Akaike's Information Criteria)

Model	AICc
EGPE	12.074
Ricker	10.97
Gompertz	12.407
Theta-L	15.395

==

Model fit of exponential growth with observation error

	Parameter estimate	Standard Error
Init_abund	3.7775785048	
Trend (mu)	-0.0720465574	0.0218640798
Sampling variance	0.068359432	
Process variance	NA: assumed = 0	

==

Model fit of exponential growth with process noise

	Parameter estimate	Standard Error
Init_abund	4.91	
Trend (mu)	-0.1280865805	0.1031663266
Sampling variance	NA: assumed = 0	
Process variance	0.1170762003	

==

Model fit of exponential growth with observation error and process noise

----

	Parameter estimate	Standard Error
Init_abund(ML)	3.7775327569	
Trend [mu(ML)]	-0.0720449931	
Sampling variance (ML)	0.056968608	
Process variance (ML)	0.0000000001	

Init_abund(REML)	4.0285257157	
Trend [mu(REML)]	-0.0953790647	0.056132318
Sampling variance(REML)	0.0439179546	
Process variance(REML)	0.0295019512	

==

Model fit of Ricker density dependent growth with process noise
----

	Parameter estimate	95% Lower C.I.	95% Upper C.I.
a_hat	0.5545029297	0.2093225381	1.0808208086
b_hat	-0.2415080287	-0.4306277829	-0.1209474678
sigma_hat	0.2595369277	0.1369360956	0.3526803471

==

Model fit of Gompertz density dependent growth with process noise
----

	Parameter estimate	95% Lower C.I.	95% Upper C.I.
a_hat	0.5068333776	0.1816265227	1.046157398
b_hat	-0.6342508799	-1.1703701546	-0.3225267201
sigma_hat	0.2770553233	0.1457821309	0.3498999459

==

Model fit of Theta-logistic density dependent growth with process noise
----

	Parameter estimate
a_hat	0.1159992976
b_hat	0.014549738
theta_hat	2.557183594
sigma_hat	0.2501186494

==

Residuals from EGPE fit

Time	Abundance	ln(Abund)	ln[Lambda(t)]	Residuals
1989	4.91	1.59127394180643	-0.687055791166543	-0.558969210710864
1990	2.47	0.904218150639886	0.125401266541272	0.253487846996952
1991	2.8	1.02961941718116	0.256854608656521	0.384941189112201
1992	3.62	1.28647402583768	-0.358254723098251	-0.230168142642571
1993	2.53	0.928219302739429	-0.126217717267401	1.86886318827809E-03
1994	2.23	0.802001585472027	0.234735299477995	0.362821879933674
1995	2.82	1.03673688495002	-2.51359732715423E-02	0.102950607184137
1996	2.75	1.01160091167848	-0.165732644100871	-3.76460636451912E-02
1997	2.33	0.845868267577609	0.265989247840521	0.394075828296201
1998	3.04	1.11185751541813	-0.64812349918599	-0.520036918730311
1999	1.59	0.46373401623214	-0.281412459438186	-0.153325878982506
2000	1.2	0.182321556793955		

Residuals from Ricker fit

Time	Abundance	ln(Abund)	ln[Lambda(t)]	Residuals
1989	4.91	1.59127394180643	-0.687055791166543	-5.57543000175069E-02
1990	2.47	0.904218150639886	0.125401266541272	0.16742316768116
1991	2.8	1.02961941718116	0.256854608656521	0.378574159264859
1992	3.62	1.28647402583768	-0.358254723098251	-3.84985889622483E-02
1993	2.53	0.928219302739429	-0.126217717267401	-6.97053344059778E-02
1994	2.23	0.802001585472027	0.234735299477995	0.218795273731736
1995	2.82	1.03673688495002	-2.51359732715423E-02	0.101413737910641
1996	2.75	1.01160091167848	-0.165732644100871	-5.60884949271466E-02
1997	2.33	0.845868267577609	0.265989247840521	0.27420002496349
1998	3.04	1.11185751541813	-0.64812349918599	-0.468442021691507
1999	1.59	0.46373401623214	-0.281412459438186	-0.451917623547499
2000	1.2	0.182321556793955		

Residuals from Gompertz fit

Time	Abundance	ln(Abund)	ln[Lambda(t)]	Residuals
1989	4.91	1.59127394180643	-0.687055791166543	-0.184622270984678
1990	2.47	0.904218150639886	0.125401266541272	0.19206904661337
1991	2.8	1.02961941718116	0.256854608656521	0.403058252377011
1992	3.62	1.28647402583768	-0.358254723098251	-4.91408178227695E-02
1993	2.53	0.928219302739429	-0.126217717267401	-4.43271853567864E-02
1994	2.23	0.802001585472027	0.234735299477995	0.23657213314875
1995	2.82	1.03673688495002	-2.51359732715423E-02	0.125581930644237
1996	2.75	1.01160091167848	-0.165732644100871	-3.09572533505152E-02
1997	2.33	0.845868267577609	0.265989247840521	0.29564856323644
1998	3.04	1.11185751541813	-0.64812349918599	-0.449760269294766
1999	1.59	0.46373401623214	-0.281412459438186	-0.494122129210293
2000	1.2	0.182321556793955		

Example output from Viable Population Monitoring with data "Bear2.xls"

Data:

Time	Abundance
1959	44
1960	47
1961	46
1962	44
.	
..	
1997	99

==

Information Theoretic Model Selection (Akaike's Information Criteria)

Model	AICc

==

Viable Population Monitoring (VPM)

Probability of reaching population size of 30 within a time period of 50

Time	Abundance	mu(EGPN)	variance(EGPN)	Probability(EGPN)	mu(EGSS)	variance(EGSS)	Probability(EGSS)
1959	44						
1960	47						
1961	46						
1962	44						
1963	46						
1964	45						
1965	46						
1966	40						
1967	39						
1968	39						
1969	42						
1970	39						
1971	41						
1972	40						
1973	33						
1974	36						
1975	34						
1976	39						
1977	35						
1978	34						
1979	38	-0.00733	0.00708	0.840179	-0.015024	0	1
1980	36	-0.009556	0.00683	0.908833	-0.01364	0.000157	1
1981	37	-0.007876	0.006567	0.867629	-0.011427	0.000532	0.993539
1982	41	-0.00307	0.006799	0.673913	-0.007067	0.001384	0.700152
1983	39	-0.005026	0.006596	0.769062	-0.006511	0.001436	0.745598
1984	51	0.005905	0.009308	0.299205	0.001713	0.003581	0.160794
1985	47	0.002537	0.009231	0.44658	0.001826	0.003458	0.21819
1986	57	0.009587	0.010218	0.18133	0.007211	0.004561	0.054431
1987	48	0.003108	0.011015	0.457287	0.003863	0.003862	0.16886
1988	60	0.010695	0.012291	0.184336	0.008067	0.0041	0.024796
1989	65	0.013007	0.012028	0.115301	0.011319	0.004746	0.011377
1990	74	0.01677	0.012066	0.050444	0.015218	0.00566	0.003957

1991	69	0.01406	0.011912	0.083924	0.014103	0.005278	0.006062
1992	65	0.011824	0.011705	0.122378	0.012194	0.005196	0.013263
1993	57	0.007614	0.011953	0.255309	0.008472	0.00587	0.078479
1994	70	0.013266	0.012719	0.098905	0.011676	0.005265	0.009725
1995	81	0.016952	0.012845	0.04191	0.015378	0.006059	0.002893
1996	99	0.021917	0.0134	0.011682	0.020667	0.008302	0.001326
1997	99	0.02134	0.013051	0.011382	0.021091	0.008222	0.001132

R Code: Density dependent state space model for population abundance data with unequal time intervals

R program to calculate maximum likelihood and restricted maximum likelihood estimates for the Ornstein Uhlenbeck state space model, using population abundance data having possibly unequal observation time intervals.

```
#  Ornstein Uhlenbeck State Space Model version date 122010.R:
#
#  Program for calculating maximum likelihood (ML) or restricted maximum
#  likelihood (REML) estimates of unknown parameters for the Ornstein
#  Uhlenbeck State Space (OUSS) model of stochastic population growth.
#  The model is
#
#  dX(t) = theta*[mu - X(t)]*dt  +  dW(t)
#          with dW(t) ~ normal(0,dt*betasq),
#  Y(t) = X(t) + F(t)
#          with F(t) ~ normal(0,tausq).
#
#  Here X(t) is log-population abundance, Y(t) is observed or estimated value
#  of X(t), theta, mu, betasq, tausq are parameters.  The parameter betasq
#  is the variance of the process noise, and tausq is the variance of the
#  observation error.
#
#  The model takes population abundance N(t) = exp(X(t)) to be governed by a
#  stochastic, continuous time density dependent model, with the observed
#  abundances O(t) = N(t)*exp(F(t)) arising from lognormal sampling error.
#
#  User provides time series of observed population abundances o(0), o(1),
#  ..., o(q), which are log-transformed by the program into y(0), y(1), ...,
#  y(q), assumed to be a time series realization of Y(t).  Likelihood
#  function of y(0), y(1), ..., y(q) is that of a multivariate normal
#  distribution.  The observation times t_0, t_1, t_2, ..., t_q can have
#  unequal intervals.
#
#  Program computes initial parameter values for iterations.  The program
#  should be re-run for several sets of initial values, as the likelihood
#  function for the model frequently has multiple local maxima.
#
#  This program written by Brian Dennis (Dept Fish and Wildlife Resources,
#  Univ Idaho, Moscow, Idaho, 83844-1136 USA  brian@uidaho.edu).
#
#  Citations:
#    Dennis, B. 2011.  Density dependent state space model for population
#    abundance data with unequal time intervals.  Unpublished manuscript
#    for:  Ecology.
#
#-----------------------------------------------------------
```

```
#        USER INPUT SECTION
#------------------------------------------------------------
# User supplies time series data here.  User can substitute R statements to
#    read population abundance data from a file into the vector "Observed.t".
#    Times of observation are entered into the vector "Time.t".

Observed.t=c(346,675,802,1478,1173,756,861,972,854,1161,1318,901,901,1173,
    608,811,903,584,1179,1020,1129,966);  # No zeros! (With zeros, you must
                             #   use another model).
Time.t=c(1956,1957,1958,1959,1960,1961,1962,1963,1964,1965,1970,1971,1972,
    1973,1974,1975,1976,1977,1978,1979,1980,1981);  # Initial time can
                             #   be nonzero.

# Example data are bobcat (Lynx rufus) in Idaho, data set 212 from the Global
# Population Dynamics Database.
#------------------------------------------------------------
#        PROGRAM INITIALIZATION SECTION
#------------------------------------------------------------
library(MASS);  # loads miscellaneous functions (ginv, etc.)
T.t=Time.t-Time.t[1]; # For calculations, time starts at zero.
Y.t=log(Observed.t);  # Log-transform the observations.
q=length(Y.t)-1;      #  Number of time series transitions, q.
qp1=q+1;             #  q+1 gets used a lot, too.
S.t=T.t[2:qp1]-T.t[1:q];  # Time intervals.


#------------------------------------------------------------
#        SECTION FOR DEFINING ML & REML LOG-LIKELIHOODS
#------------------------------------------------------------


# ML objective function "negloglike.OU.ml" is negative of log-likelihood;
# the Nelder-Mead optimization routine in R, "optim", is a minimization
# routine.  The ML objective function uses a multivariate normal log-
# likelihood (Eq. 16 in Dennis 2010).  The three function arguments are:
# phi, vector of parameters (transformed to the real line),
# yt, vector of time series observations,
# tt, vector of observation times.

negloglike.OU.ml=function(phi,yt,tt)
{
  mu=phi[1];
  theta=exp(phi[2]);         #  Constrains theta > 0.
  betasq=exp(phi[3]);      #  Constrains betasq > 0.
  tausq=exp(phi[4]);       #  Constrains tausq > 0.
  thing=betasq/(2*theta);   #  Recurring quantity.
  ss=tt[2:qp1]-tt[1:q];     #  Time intervals.
  q=length(yt)-1;
  qp1=q+1;
  vx=matrix(1,qp1,qp1);  # Preallocate matrix for autocorrelations.
  #  Following loop calculates the model autocorrelations and puts
  #    them in vx.
  for (ti in 1:q)
  {
    vx[(ti+1):qp1,ti]=exp(-theta*cumsum(ss[ti:q]));
    vx[ti,(ti+1):qp1]=vx[(ti+1):qp1,ti];
  }
```

```r
    Sigma.mat=vx*thing;   #  Variance-covariance matrix for X(t).
    Itausq=matrix(0,qp1,qp1);
    diag(Itausq)=rep(tausq,qp1);
    V=Sigma.mat+Itausq;   #  Variance-covariance matrix for Y(t).
    mm=rep(mu,qp1);
    ofn=(qp1/2)*log(2*pi)+0.5*log(det(V))+
       0.5*(yt-mm)%*%ginv(V)%*%(yt-mm);
    return(ofn);
}

#  REML objective function "negloglike.OU.reml" is negative of log-likelihood
#  for first differences of the log-scale observations.  The REML objective
#  function uses equations 17-19 of Dennis (2010).  The three
#  function arguments are:
#  phi, vector of parameters (transformed to the real line),
#  yt, vector of time series observations (log scale),
#  tt, vector of observation times.
#  The function performs the differencing.
negloglike.OU.reml=function(phi,yt,tt)
{
    theta=exp(phi[1]);        #  Constrains th > 0.
    betasq=exp(phi[2]);      #  Constrains betasq > 0.
    tausq=exp(phi[3]);       #  Constrains tausq > 0.
    thing=betasq/(2*theta);      #  Recurring quantity.
    ss=tt[2:qp1]-tt[1:q];       #  Time intervals.
    q=length(yt)-1;
    qp1=q+1;
    vx=matrix(1,qp1,qp1); # Preallocate matrix for autocorrelations.
    #  Following loop calculates the autocorrelations and puts
    #     them in vx.
    for (ti in 1:q)
    {
       vx[(ti+1):qp1,ti]=exp(-theta*cumsum(ss[ti:q]));
       vx[ti,(ti+1):qp1]=vx[(ti+1):qp1,ti];
    }
    Sigma.mat=vx*thing;
    Itausq=matrix(0,qp1,qp1);
    diag(Itausq)=rep(tausq,qp1);
    V=Sigma.mat+Itausq;
    Dmat=cbind(-diag(1,q),matrix(0,q,1))+
       cbind(matrix(0,q,1),diag(1,q));   #  Differencing matrix.
    Phi.mat=Dmat%*%V%*%t(Dmat);          #  REML var-cov mattrix.
    wt=yt[2:qp1]-yt[1:q];
    ofn=(q/2)*log(2*pi)+0.5*log(det(Phi.mat))+
       0.5*wt%*%ginv(Phi.mat)%*%wt;
    return(ofn);
}

#-----------------------------------------------------------
#       SECTION FOR CALCULATING INITIAL VALUES.
#-----------------------------------------------------------
Ybar=mean(Y.t);
Yvar=sum((Y.t-Ybar)*(Y.t-Ybar))/q;

mu1=Ybar;
```

```
th1=-mean(log(abs((Y.t[2:qp1]-mu1)/
   (Y.t[1:q]-mu1)))/S.t);          # Kludge an initial value for theta
                                   #  based on mean of Y(t+s) given Y(t).
bsq1=2*th1*Yvar/(1+2*th1);        #  Moment estimate using stationary
tsq1=bsq1;                        #   variance, with betasq=tausq.

#----------------------------------------------------------------------
#        SECTION FOR CALCULATING ML & REML PARAMETER ESTIMATES
#----------------------------------------------------------------------

# The ML estimates.
OUSSml=optim(par=c(mu1,log(th1),log(bsq1),log(tsq1)),
   negloglike.OU.ml,NULL,method="Nelder-Mead",yt=Y.t,tt=T.t);
params.ml=c(OUSSml$par[1],exp(OUSSml$par[2]),exp(OUSSml$par[3]),
   exp(OUSSml$par[4]));
lnlike.ml=-OUSSml$value[1];
AIC.ouss=-2*lnlike.ml+2*length(params.ml);

mu.ml=params.ml[1];           # These are the ML estimates.
theta.ml=params.ml[2];        #         --
betasq.ml=params.ml[3];       #          --
tausq.ml=params.ml[4];        #          --

# The REML estimates.
OUSSreml=optim(par=c(log(th1),log(bsq1),log(tsq1)),
   negloglike.OU.reml,NULL,method="Nelder-Mead",yt=Y.t,tt=T.t);
params.reml=c(exp(OUSSreml$par[1]),exp(OUSSreml$par[2]),
   exp(OUSSreml$par[3]));
theta.reml=params.reml[1];    #  These are the REML estimates.
betasq.reml=params.reml[2];   #         --
tausq.reml=params.reml[3];    #          --

#  Calculate REML estimate of mu using Eq. 20 of Dennis (2010).
thing=betasq.reml/(2*theta.reml);
vx=matrix(1,qp1,qp1);
for (ti in 1:q)
{
   vx[(ti+1):qp1,ti]=exp(-theta.reml*cumsum(S.t[ti:q]));
   vx[ti,(ti+1):qp1]=vx[(ti+1):qp1,ti];
}
Sigma.mat=vx*thing;
Itausq=matrix(0,qp1,qp1);
diag(Itausq)=rep(tausq.reml,qp1);
V.reml=Sigma.mat+Itausq;
j=matrix(1,qp1,1);
Vinv=ginv(V.reml);
mu.reml=(t(j)%*%Vinv%*%Y.t)/(t(j)%*%Vinv%*%j);  #  REML estimate of mu.

Var_mu.reml=1/(t(j)%*%Vinv%*%j);        #  Variance of mu
mu_hi.reml=mu.reml+1.96*sqrt(Var_mu.reml); #  95% CI for mu
mu_lo.reml=mu.reml-1.96*sqrt(Var_mu.reml); #       --

#  Calculate predicted population sizes for the OUSS model
#  (X(tj) given all the observations except for Y(tj))
#  with multivariate normal distribution, for plotting.
```

```
#
#  Choose ML or REML estimates here (by commenting out the unwanted).
#  mu=mu.ml;  theta=theta.ml;  betasq=betasq.ml;  tausq=tausq.ml;
mu=mu.reml;  theta=theta.reml;  betasq=betasq.reml;  tausq=tausq.reml;

thing=betasq/(2*theta);
vx=matrix(1,qp1,qp1);
for (ti in 1:q)
{
   vx[(ti+1):qp1,ti]=exp(-theta*cumsum(S.t[ti:q]));
   vx[ti,(ti+1):qp1]=vx[(ti+1):qp1,ti];
}
Sigma.mat=vx*thing;
Itausq=matrix(0,qp1,qp1);
diag(Itausq)=rep(tausq,qp1);
V=Sigma.mat+Itausq;

Predict.t=rep(0,qp1);
Muvec=rep(mu,q);
for (tj in 1:qp1)
{
Y.omitj=Y.t[-tj];    #  Omit observation at time tj.
V.omitj=V[-tj,-tj];  #  Omit row tj and col tj from var-cov matrix.
V12=V[tj,-tj];       #  Submatrix:  row tj without col tj.
Predict.t[tj]=mu+V12%*%ginv(V.omitj)%*%(Y.omitj-Muvec);  #  Usual expression
                                    #  for conditional
                                    #  MV normal mean.
}
Predict.t=exp(Predict.t);

# Plot the data & model-fitted values
plot(Time.t,Observed.t,xlab="time",ylab="population abundance",
   type="o",pch=1,cex=1.5);      #  Population data are circles.
par(lty="dashed");               #  Predicted abundances are dashed line.
points(Time.t,Predict.t, type="l", lwd=1);

# Print the parameter estimates
parms.reml=c(mu.reml,theta.reml, betasq.reml,tausq.reml); #  Collect for
                                    #    printing.
parms.ml=c(mu.ml,theta.ml, betasq.ml,tausq.ml);          #    --
names=c("mu","theta","betasq","tausq");                  #    --
types=c("OUSS-ML","OUSS-REML");                          #    --
matrix(cbind(parms.ml,parms.reml),
   nrow=2,ncol=4,byrow=TRUE,dimnames=list(types,names));      #  Print stuff

matrix(cbind(mu_lo.reml,mu_hi.reml),nrow=1,ncol=2,byrow=TRUE,
   dimnames=list("95% CI for MU",c("LO","HI")));             #  Print stuff

matrix(cbind(lnlike.ml,AIC.ouss),nrow=1,ncol=2,byrow=TRUE,
   dimnames=list("OUSS ML RESULTS",c("LN-LIKELIHOOD","AIC"))); #  Print stuff
```

OUTPUT:
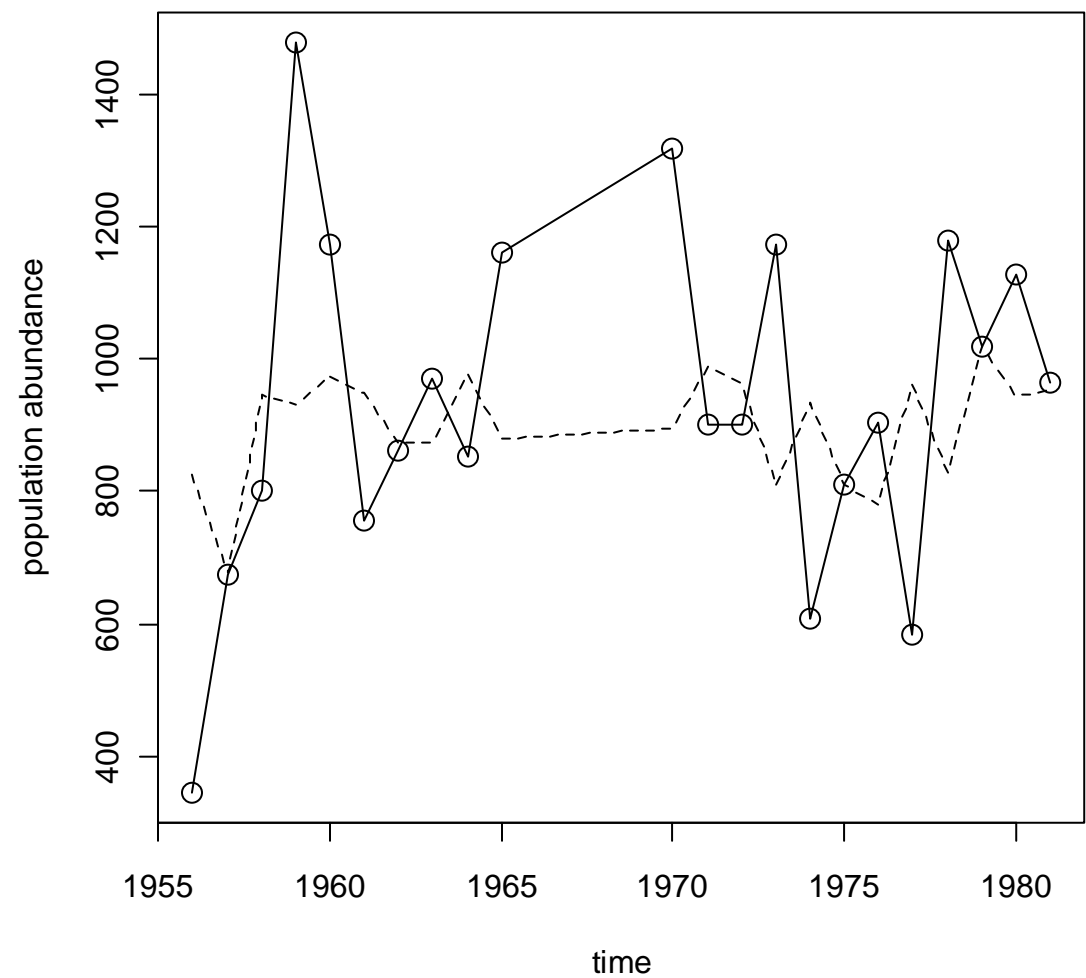
	mu	theta	betasq	tausq
OUSS-ML	6.794726	1.692528	0.3339971	0.0001871666
OUSS-REML	6.792985	1.259853	0.2717515	0.0007480839

	LO	HI
95% CI for MU	6.615151	6.97082

	LN-LIKELIHOOD	AIC
OUSS ML RESULTS	-5.394046	18.78809

R Code: Fitting population growth models and projecting future Sonoran pronghorn viability.

```
# Simulation Setup
#-----------------------------------------------------
library(MASS)
NumReps = 4000

NumTimeSteps = 20
WildSexRatio = .5                     #Female/(Females+Males) sex ratio
InitAbund1 = 34                       #Number of females in captive pen in 2009
InitAbund2 = 68                       #Number of individuals in wild population in 2008
InitAbund2 = InitAbund2*WildSexRatio  #Number of females in wild population
InitAbund3 = 0                        #Intitial abund. of reestablished population
InitAbund3 = InitAbund3*WildSexRatio

lambdamax = 2  #1.86 highest observed in captive population; 3 highest biological = 2 fawns:doe,
        100% survival adults and fawns
Pop1_K = 34
Pop2_K = 282*WildSexRatio             #Highest observed abundance in current wild population
Pop3_K = 282*WildSexRatio             #Highest observed abundance in current wild population

WildsCorrelation = .5                 #Correlation between Pop2 and Pop3 in residual variance of
        growth models

NoParamEstError = F
NoPrecipError = F                     #for stochastic future precipitation
NoResidualError = F                   #for stochastic pop. growth

PrecipIntercept = 12.3                #avg. biannual precip from Organ Pipe, Tacna3, Ajo (1993-
        2008)
PrecipBetaYear = 0                    #linear trend in precipitation
sdPrecip = 4.04                       #residual error in precip. model
#=========================================================

if (NoPrecipError==T)sdPrecip=0
PrecipDeviate_t=matrix(rnorm(NumReps*NumTimeSteps,0,sdPrecip),NumReps,NumTimeSteps)

Time_t = 0:NumTimeSteps
NumAbund = NumTimeSteps+1
NPop1 = matrix(0,NumReps,NumAbund)
NPop2 = matrix(0,NumReps,NumAbund)
NPop2with3 = matrix(0,NumReps,NumAbund)
NPop3 = matrix(0,NumReps,NumAbund)

Emigrants = matrix(0,NumReps,NumAbund)
CurrentPrecip=matrix(0,NumReps,NumAbund)

lambda1 = matrix(0,NumReps,NumTimeSteps)
lambda2=matrix(0,NumReps,NumTimeSteps)
lambda2with3=matrix(0,NumReps,NumTimeSteps)
lambda3=matrix(0,NumReps,NumTimeSteps)

BootBeta_0 = array(0,NumReps)
BootBeta_lnN = array(0,NumReps)
BootBeta_Precip = array(0,NumReps)
BootSigma2 = array(0,NumReps)

#=============================================================
# Estimate Population 1 Growth Parameters (Captive Population)
#-----------------------------------------------------
Nt_1 = c(6,11,17,24,34)                        #Female abundance data from CPNWR captive pop.
Ntplus1_1 = c(8,14,24,34,41)
rt_1 = log(Ntplus1_1/Nt_1)

mu1 = mean(rt_1)                        #Exponential Growth Model
sigma1 = sd(rt_1)
SE_mu = sqrt(sigma1^2/length(rt_1))

#-----------------------------------------------------
# Create random deviates
```

```
#--------------------------------------------------
if (NoParamEstError==T)SE_mu=0
mu_rep = matrix(rnorm(NumReps,mu1,SE_mu),NumReps,1)

sigma_sq_devs = rchisq(n=NumReps,df = (length(rt_1)-1))
sigma_rep = matrix(sqrt(sigma_sq_devs*sigma1^2/(length(rt_1)-1)), NumReps,1)
if (NoParamEstError==T)sigma_rep = matrix(sigma1, NumReps,1)

E1_t = matrix(rnorm(NumReps*NumTimeSteps,0,1),NumReps,NumTimeSteps) #Standard normal deviates
if (NoResidualError==T)E1_t = matrix(0,NumReps,NumTimeSteps)
#============================================================
# Estimate Population 2 and 3 Growth Parameters
#--------------------------------------------------
Nt_2 = c(179,282,130,142,99,21,58,68)                    #Abundance data from wild pop.
Ntplus1_2 = c(282,130,142,99,21,58,68,68)
Nt_2 = Nt_2*WildSexRatio
Ntplus1_2 = Ntplus1_2*WildSexRatio

rt_2 = log(Ntplus1_2/Nt_2)
Precip = c(18.75,6.59,14.18,11.2,7.73,15.8,10.99,13.17)      #biannual precip from Organ Pipe,
       Tacna3, Ajo (1993-2008)

PrecipFit = lm (rt_2~log(Precip))
Beta_0 = coef(PrecipFit)[[1]]
Beta_lnN = 0
Beta_Precip = coef(PrecipFit)[[2]]
Q = length(rt_2)-df.residual(PrecipFit)+1
sigma2 = sqrt(anova(PrecipFit)[(Q-1),2]/length(rt_2))
bootsigma2 = sigma2

#--------------------------------------------------
# Create random deviates
#--------------------------------------------------
if (NoResidualError==T)sigma2=0
Covariance = matrix(c(1,WildsCorrelation,WildsCorrelation,1),2,2)
Devs2and3 = mvrnorm(n=NumReps*NumTimeSteps,mu = rep(0,2),Sigma=Covariance)
E2_t = matrix(Devs2and3[,1],NumReps,NumTimeSteps)                      #Standard normal deviates
E3_t = matrix(Devs2and3[,2],NumReps,NumTimeSteps)                      #Standard normal deviates

#============================================================
# Population Projection
#--------------------------------------------------

Pop2NumTimeSteps = NumTimeSteps/2
for (repj in 1:NumReps){
  NPop1[repj,1]=InitAbund1
  NPop2[repj,1]=InitAbund2
  NPop2with3[repj,1]=InitAbund2
  NPop3[repj,1]=InitAbund3

  #Get parameter estimates for for projections
  mu_j = mu_rep[repj,1]
  sig_j = sigma_rep[repj,1]

  #Parametric bootstrap time series to refit growth model for wildl pops. growth parameters
   if (NoParamEstError==F){
          NormDev = rnorm(length(Nt_2))
          BootTimeSeries = array(0,length(Nt_2)+1)
          BootTimeSeries[1]=Nt_2[1]
          for (ti in 1:length(Nt_2)){
              lambda =
        exp(Beta_0+Beta_lnN*log(BootTimeSeries[ti])+Beta_Precip*log(Precip[ti])+NormDev[ti]*boots
        igma2)
              BootTimeSeries[ti+1]=BootTimeSeries[ti]*lambda
          }
          BootNt_2=BootTimeSeries[1:length(BootTimeSeries)-1]
          BootRt_2=log(BootTimeSeries[2:length(BootTimeSeries)])-log(BootNt_2)
          BootPrecipFit = lm (BootRt_2~log(Precip))
          BootBeta_0[repj] = coef(BootPrecipFit)[[1]]
          BootBeta_lnN[repj] = 0
          BootBeta_Precip[repj] = coef(BootPrecipFit)[[2]]
```

```
           BootQ = length(rt_2)-df.residual(BootPrecipFit)+1
           BootSigma2[repj] = sqrt(anova(BootPrecipFit)[(Q-1),2]/length(rt_2))
    }

#--------------------------------------------------
#Project Wild and Captive Pops. with no Immigrants/Emigrants >> Pop1 and Pop2 get truncated to K
#--------------------------------------------------
        for (t in 2:NumAbund){
           lambda1[repj,t-1] = exp(mu_j+sig_j*E1_t[repj,t-1])
           if(lambda1[repj,t-1]>lambdamax)lambda1[repj,t-1]=lambdamax
           NPop1[repj,t] = NPop1[repj,t-1]*lambda1[repj,t-1]
           if(NPop1[repj,t]>Pop1_K){
                Emigrants[repj,t]=NPop1[repj,t]-Pop1_K
                NPop1[repj,t]=Pop1_K
           } # end if Pop1 > K

           #Grow 2nd population only in odd years
           if (t %% 2==1){
           CurrentPrecip[repj,t] = PrecipIntercept +
        PrecipBetaYear*(t+2007)+PrecipDeviate_t[repj,t-2]
           if (CurrentPrecip[repj,t]<0)CurrentPrecip[repj,t]=0.01
           if (NoParamEstError==T){
                BootBeta_0[repj]=Beta_0
                BootBeta_lnN[repj]=Beta_lnN
                BootBeta_Precip[repj]=Beta_Precip
                BootSigma2[repj]=sigma2
           }

           lambda2[repj,t-2] = exp(BootBeta_0[repj]+BootBeta_lnN[repj]*log(NPop2[repj,t-2])
        +BootBeta_Precip[repj]*log(CurrentPrecip[repj,t])
                +E2_t[repj,t-2]*BootSigma2[repj])
           if(lambda2[repj,t-2]>(lambdamax^2))lambda2[repj,t-2]=(lambdamax^2)  #wild pop grows
        every 2 years
             NPop2[repj,t] = NPop2[repj,t-2]*lambda2[repj,t-2]
#------------------
             if (NPop2[repj,t]>Pop2_K)NPop2[repj,t]=Pop2_K
#------------------
           NPop2[repj,t-1]=mean(c(NPop2[repj,t],NPop2[repj,t-2]))
           } #end if odd years

        } #end time loop
} #end replication loop

CaptiveNoMove = NPop1
Wild2NoMove = NPop2

#--------------------------------------------------
#Project Wild Pops. with Immigrants/Emigrants
#--------------------------------------------------

for (repj in 1:NumReps){
  NPop2[repj,1]=InitAbund2
  NPop2with3[repj,1]=InitAbund2
  NPop3[repj,1]=InitAbund3

for (t in 2:NumAbund){
#Grow 2nd and 3rd populations only in odd years
if (t %% 2==1){
        NtPlusE_2 = NPop2[repj,t-2]
        NtPlusE_2with3 = NPop2with3[repj,t-2]
        NtPlusE_3 = NPop3[repj,t-2]

        #------------------------------------
        #MetaPop Dynamics move individuals among populations
        #------------------------------------
        NtPlusE_2 = NPop2[repj,t-2]+Emigrants[repj,t-1]+Emigrants[repj,t]
        if (NPop2with3[repj,t-2]<140*WildSexRatio){ #If Pop2 is <140, then send emigrants to
        Pop2, otherwise send to Pop3
                NtPlusE_2with3 = NPop2with3[repj,t-2] + Emigrants[repj,t-1]+Emigrants[repj,t]
        }
        if (NPop2with3[repj,t-2]>140*WildSexRatio){
```

```
                        NtPlusE_3 = NPop3[repj,t-2] + Emigrants[repj,t-1]+Emigrants[repj,t]
        }

        #-----------------------------------
        #Grow populations
        #-----------------------------------

          if (NoParamEstError==T){
                BootBeta_0[repj]=Beta_0
                BootBeta_lnN[repj]=Beta_lnN
                BootBeta_Precip[repj]=Beta_Precip
                BootSigma2[repj]=sigma2
          }

        lambda2[repj,t-2] =
        exp(BootBeta_0[repj]+BootBeta_lnN[repj]*log(NtPlusE_2)+BootBeta_Precip[repj]*log(CurrentP
        recip[repj,t])
                +E2_t[repj,t-2]*BootSigma2[repj])
        if(lambda2[repj,t-2]>(lambdamax^2))lambda2[repj,t-2]=(lambdamax^2)
        NPop2[repj,t] = NtPlusE_2*lambda2[repj,t-2]
#------------------
        if(NPop2[repj,t]>Pop2_K)NPop2[repj,t]=Pop2_K
#------------------
        NPop2[repj,t-1]=mean(c(NPop2[repj,t],NPop2[repj,t-2]))

        lambda2with3[repj,t-2] =
        exp(BootBeta_0[repj]+BootBeta_lnN[repj]*log(NtPlusE_2with3)+BootBeta_Precip[repj]*log(Cur
        rentPrecip[repj,t])
                +E2_t[repj,t-2]*BootSigma2[repj])
        if(lambda2with3[repj,t-2]>(lambdamax^2))lambda2with3[repj,t-2]=(lambdamax^2)
        NPop2with3[repj,t] = NtPlusE_2with3*lambda2with3[repj,t-2]
#------------------
        if(NPop2with3[repj,t]>Pop2_K)NPop2with3[repj,t]=Pop2_K
#------------------
        NPop2with3[repj,t-1]=mean(c(NPop2with3[repj,t],NPop2with3[repj,t-2]))

        if (NtPlusE_3>0){
                lambda3[repj,t-2] =
        exp(BootBeta_0[repj]+BootBeta_lnN[repj]*log(NtPlusE_3)+BootBeta_Precip[repj]*log(CurrentP
        recip[repj,t])
                +E3_t[repj,t-2]*BootSigma2[repj])
        }
        if (NtPlusE_3==0)lambda3[repj,t-2]=0
        if(lambda3[repj,t-2]>(lambdamax^2))lambda3[repj,t-2]=(lambdamax^2)
        NPop3[repj,t] = NtPlusE_3*lambda3[repj,t-2]
#------------------
        if(NPop3[repj,t]>Pop3_K)NPop3[repj,t]=Pop3_K
#------------------
        NPop3[repj,t-1]=mean(c(NPop3[repj,t],NPop3[repj,t-2]))

} #end if odd years

} #end time loop
} #end replication loop

Wild2MoveNo3 = NPop2
Wild2MoveWith3 = NPop2with3
Wild3Move = NPop3
WildTotalMove = Wild2MoveWith3+Wild3Move

#--------------------------------------------------
# Output
#--------------------------------------------------

# Deterministic
#--------------------------------------------------
if (NoParamEstError==T){
if (NoPrecipError==T){
if (NoResidualError==T){
```

```
xrange <- range(Time_t)
yrange <- c(0,max(Wild2NoMove,Wild2MoveNo3,WildTotalMove))
plot(xrange, yrange, type = 'n', xlab = 'Years Into Future', ylab = 'Female Abundance', yaxs="i",
        xaxs="i", bty="l")
        for (j in 1:NumReps) {
        lines(Time_t,Wild2NoMove[j,], col = "black", lwd = 1, lty=2,yaxs="i", xaxs="i")
        lines(Time_t,Wild2MoveNo3[j,],col="black", lwd = 2, lty=1,yaxs="i", xaxs="i")
        lines(Time_t,WildTotalMove[j,],col="black", lwd = 3, lty=3,yaxs="i", xaxs="i")
#       lines(Time_t,Wild3Move[j,],col="black", lwd = 3, lty=3, yaxs="i", xaxs="i")
        }
}
}
}

# Stochastic
#---------------------------------------------
y1 = Wild2NoMove[,NumAbund]
y2 = Wild2MoveNo3[,NumAbund]
y3 = Wild2MoveWith3[,NumAbund]
y4 = Wild3Move[,NumAbund]
y5 = WildTotalMove[,NumAbund]

xrange=c(0,400) #range(c(WildOnly, x2)
yrange=c(0,0.04)
plot(density(y1), col = "black",xlim=xrange, ylim=yrange,yaxp = c(0,0.035,1),
        main="", ylab = "Probability density", xlab="Final Abundance", lty=2, lwd = 1,xaxs="i",
        yaxs="i", bty="l")
lines (c(26.57, 26.57), c(0,1), lty = 2, lwd =1, xaxs="i", yaxs="i")

lines(density(y2), col="black", lwd = 2,lty=1,xaxs="i", yaxs="i")
lines (c(141,141),c(0,1),lwd=2,lty=1,xaxs="i", yaxs="i")

lines(density(y5), col="black", lwd = 3,lty=3,xaxs="i", yaxs="i")
lines (c(220,220),c(0,1),lwd=3,lty=3,xaxs="i", yaxs="i")


wildonlyvar = var(y1)  #Wild Only Variance
wildmetapopvar =var(y5)  #Wild Metapop Variance

less50WildOnly = y1<50
ProbLess50WildOnly = sum(less50WildOnly)/NumReps
more100WildOnly = y1>100
ProbMore100WildOnly = sum(more100WildOnly)/NumReps

less50Wild2No3 = y2<50
ProbLess50Wild2No3 = sum(less50Wild2No3)/NumReps
more100Wild2No3 = y2>100
ProbMore100Wild2No3 = sum(more100Wild2No3)/NumReps

less50Wild2and3 = y5<50
ProbLess50Wild2and3 = sum(less50Wild2and3)/NumReps
more100Wild2and3 = y5>100
ProbMore100Wild2and3 = sum(more100Wild2and3)/NumReps

ProbLess50WildOnly
ProbLess50Wild2No3
ProbLess50Wild2and3
ProbMore100WildOnly
ProbMore100Wild2No3
ProbMore100Wild2and3
wildonlyvar
wildmetapopvar
```